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PHYTOLOGIA

An international journal to expedite plant systematic, phytogeographical
and ecological publication

Vol. 84

April 1998

No. 4

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QUALITY CHANGE OF HABITAT IN NORTHWESTERN LOUISIANA

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ABSTRACT

We revisited twenty botanically significant sites in Caddo Parish that we have known for twenty or more years where important botanical collections had been made. We compared the condition of those sites twenty years ago to what they are today. We found an overall deterioration in site quality of 47% in twenty years. One site had improved in quality, one had remained the same, and eighteen had deteriorated. Most of the deterioration has been caused by urban development and agroforestry.

KEY WORDS: Louisiana, habitat deterioration, ecology

INTRODUCTION

A recent worldwide study by the World Conservation Monitoring Center (1997) found that 12% of all vascular flora is either extinct or on the verge of distinction. The reason is habitat destruction. The *Living Planet Report 1998* produced by the World Wildlife Fund for Nature, the New Economics Foundation, and the World Conservation Monitoring Center, found that since 1970 humans have destroyed 30% of the natural world, and since 1990 the rate of destruction has increased to about 3% per year.

The overall destruction and degradation of the natural habitat of the eastern and southeastern United States have been well documented (Frost 1993; Martin & Boyce 1993; Boyce & Martin 1993; Whitney 1994; Noss *et al.* 1995). After four centuries of European presence, even the most conservative estimates of natural habitat remaining indicate its future is very precarious. Many historic plant communities have ceased to exist, and others hang in the balance. Very few examples exist in pristine condition.

The degrading of these natural communities continues. Estimates of rate of deterioration and destruction vary depending on measurement criteria. If "pristine" were taken to be the criterion, then almost none exists. If "relatively natural condition" meaning "areas that have been repeatedly cut over but retain some semblance of originality," (Louisiana Natural Heritage Program 1993) is used, then some exist, but even here very little.

Using the Louisiana Natural Heritage figures, which that agency admits to be "not very satisfactory" (Louisiana Natural Heritage Program 1993) but which are at least conservative, and combining all plant communities together, no more than 30% of Louisiana's natural communities exists in "relatively natural condition." Some communities are totally gone and others are on the brink of extinction.

An example, well documented because of economic importance, is the vast longleaf pine forests that once characterized much of the West Gulf Coastal Plain. These were reduced to 22% of their original extent by 1935, and today only 12% of that 22% remains (Outcalt 1997), most in very poor condition.

We have been botanizing in Louisiana for over twenty years. We have visited the same sites repeatedly. Because little is known about the rate of regional deterioration of the natural landscape, we decided to assess the current quality of several of these sites and compare their present condition with what it was twenty years ago.

STUDY AREAS AND METHODS

Caddo Parish is located in the northwestern corner of Louisiana with Texas to the west, Arkansas to the north, and the Red River to the east. The parish consists of 882 square miles, measuring approximately 60 miles north-south and 15 miles east-west. The coordinates 33° N 94° W cross near the northwest corner of the parish. MacRoberts (1979) and Teague & Wendt (1994) provide information on geology, soils, climate, topography, land use history, and present and past vegetation and communities.

Present plant communities broadly fall into shortleaf pine-oak-hickory forests in the uplands and various bottomland hardwood and swamp forests along the Red River and its tributaries. Within this broad classification various natural plant communities occur, many of which are classified as rare or endangered statewide and a few of which are known now only from historical accounts (Teague & Wendt 1994; MacRoberts *et al.* 1997). Since about 1830 when Europeans first began settling the area, Caddo Parish has been intensively logged, grazed, and farmed: first along the Red River and then in the uplands. The oil and gas industry also has left its mark. The Red River is now dammed.

The study sites are scattered over the parish both north and south of Shreveport, a city of 200,000 located in the south. Three sites are in Shreveport itself. Most of the sites are in the uplands, the flood plain having been drastically altered long ago by intensive agriculture and grazing, which continues today. The sites were not chosen to

survey all community types. Also, twenty is such a small number that an analysis of relative change by community is unprofitable.

Because we did not plan this study twenty years ago, we must proceed using a rather subjective approach. However, this may not be as bad as it sounds since many of the sites are obviously destroyed and others are clearly degraded. Given this caveat, the problem remains of deciding just how changed a site is. Our criterion was to compare how a site looked today to the way it looked twenty years ago. We attempted to estimate the change in natural diversity, change in size, and change in overall condition. If a site has become a subdivision, we gave it a -100% score. If it was a hardwood forest twenty years ago and now is a clearcut, site-prepared loblolly pine plantation, it also received a -100%. If it has become an overgrown tangle because of fire suppression, we considered it only marginally changed. If it has been criss-crossed with roads preparatory of a subdivision, we estimated damage at the present time.

None of the sites were undisturbed when first visited; at best, all were in "relatively natural condition." So we are not talking about the rate of change from a pristine or pre-European condition but from a condition twenty years ago, whatever that condition was. Twenty years ago these areas were some of the best sites for the local flora.

All sites used in this sample were chosen not only because we had first-hand knowledge of them but because they had been the sites of important collections of rare Louisiana species, for example, *Astragalus soxmaniorum* Lundell, *Ceanothus herbaceus* Raf., *Dentaria laciniata* Muhl. ex Willd., *Draba cuneifolia* Nutt. ex Torr. & Gray, *Erythronium albidum* Nutt., *Coreopsis intermedia* Sherff, *Dalea villosa* (Nutt.) Spreng. var. *grisea* (Torr. & Gray) Barneby, *Dalea phleoides* (Torr. & Gray) Shinnars, *Erythronium longifolium* Nutt., *Isotria verticillata* (Muhl. ex Willd.) Raf., *Mirabilis albida* (Walt.) Heimerl, *Penstemon murrayanus* Hook., *Phacelia strictiflora* (Engelm. & Gray) A. Gray, *Platanthera lacera* (Michx.) G. Don, *Polygonella americana* (Fisch. & Mey.) Small, *Psoralea subulata* Bush, *Quercus arkansana* Sarg., *Ribes curvatum* Small, *Selaginella arenicola* Underw. subsp. *riddellii* (Van Estelt.) R. Tyson, *Tetragonotheca ludoviciana* (Torr. & Gray) A. Gray ex Hall, *Trillium recurvatum* Beck, *Trillium texanum* Buckl., *Zigadenus nuttallii* (A. Gray) S. Wats., and *Zornea bracteata* J.F. Gmel. (MacRoberts 1979; MacRoberts 1989; Thomas & Allen 1993-1998; Louisiana Natural Heritage Program 1995). A number of these are (or have been) ranked as Federal candidate species, and most are ranked as state rare or endangered.

For this analysis, we visited the sites in the spring of 1998 and assessed their current quality.

RESULTS

Table 1 summarizes the survey results of the twenty Caddo Parish sites examined in this study.

Table 1. Site name, location, percentage change, and reason for change.

| Site | Change % | Location and Condition |
|------|----------|--|
| 1) | -50 | T17N R14W Sec. 13. Betty Virginia Park hardwood bluff. Land cleared. |
| 2) | -90 | T16N R13W Sec. 16. <i>Psoralea</i> sandylands. Land cleared and converted to lawn. |
| 3) | -90 | T17N R13W Sec. 31. Spring Lake Estates pine/hardwoods. Developed with a few lots left. |
| 4) | -100 | T16N R13W Sec. 17. <i>Platanthera lacera</i> mesic hardwood site. Subdivision, nothing left. |
| 5) | -20 | T16N R13W Sec. 30. Gowan Place calcareous prairie remnant. Fire suppressed and overgrown. |
| 6) | 0 | T15N R13W Sec. 2. Wallace Lake Dam riparian. Corps of Engineers dam area. Federal land. |
| 7) | -50 | T16N R13W Sec. 7-8. YMCA Camp pine/hardwoods. Pines removed. |
| 8) | -50 | T16N R13W Sec. 6. Ellerbe Rd. pine/hardwoods. Half developed as sub-division. |
| 9) | -20 | T22N R15W Sec. 22. <i>Erythronium</i> pine/hardwoods. Land scraped, roads for subdivision. |
| 10) | -30 | T22N R15W Sec. 14. Bluff hardwoods. Some lumbering. |
| 11) | -100 | T23N R15W Sec. 26. Red House sandylands. House and yard on site. |
| 12) | -100 | T22N R16W Sec. 11. Kendrick Road sandylands. House and yard on site. |
| 13) | -20 | T23N R15W Sec. 26. Ida sandylands. Shrub encroachment, fire suppression. |
| 14) | -50 | T22N R15W Sec. 4. <i>Isotria</i> place. Mesic pine-hardwoods. Pines cut out, site trashed. |
| 15) | -40 | T23N R16W Sec. 21. <i>Quercus arkansana</i> sandylands. Fire suppression and grazing. |
| 16) | -100 | T22N R15W Sec. 33. <i>Trillium</i> mesic hardwoods. Hardwood riparian, clearcut, pine plantation. |
| 17) | -50 | T21N R16W Sec. 16. <i>Talinum</i> sandylands. Clear cut, some some hardwoods left. |
| 18) | -20 | T21N R16W Sec. 23. Roger's Station sandylands. Bulldozer scrapings. |
| 19) | +50 | T18N R13W Sec. 32. V.A. Hospital hardwood bluff. Understory opened and overstory left. Federal land. |
| 20) | -10 | T18N R13W Sec. 31. Greenwood Cemetery <i>Zigadenus</i> site. Mowed prairie with grave encroachment. |

Average -47

DISCUSSION

Of the twenty sites, eighteen have deteriorated in twenty years, one has remained the same, and one has improved. Four sites had been totally destroyed. The deterioration is 47% overall or an average of about 2.3% per year. Applying a simple Sign Test to these data indicates that the probability of obtaining this distribution is $p < .001$, with the direction of change for the botanical worse.

Bridges (1988:4), in his study of longleaf pine savannas in southwestern Louisiana, found that "perhaps as many as ten percent of the total areas identified had lowered in quality during the intervening $2\frac{1}{2}$ years due primarily to timber management," a figure not dissimilar to that reported here. Bridges (1988:4) gives what he calls an "extreme example," one which he says undoubtedly has been repeated countless times over the last few decades: "a longleaf pine savanna which had fairly large trees on the aerial in 1985, was good quality and maintained by fire when driven by in 1987, on April 11, 1988 it was noted that the site had been thinned removing most trees over 12 [inches] dbh but leaving the remaining longleaf pines intact, on May 22, 1988 a species list was made of the fairly representative savanna flora of this certainly recoverable site, on May 24, 1988 during another drive-by bulldozers were pushing the remaining trees into piles and scraping the ground clean, and on June 11, 1988 the site was an open field which had been seeded for improved pasture." Four of our examples were altered to this extreme.

The Louisiana Natural Heritage (1993) gives percentage estimates of acreage remaining in "relatively natural condition" in Louisiana. They suggest that no more than 30% exists in this condition, which means that there is very little land remaining of any botanical quality whatsoever. Even accepting the above figure, which we consider to be an overestimate for northwestern Louisiana, if our data are correct, about half the natural landscape has been lost in the last twenty years.

Interestingly, neither of the federally owned sites in our study (sites 6 and 19) had deteriorated. One is a Corps of Engineers Dam at Wallace Lake, which continues to be riparian, floodplain, and pasture. It was not in "relatively natural condition" twenty years ago, but it is basically as it was then.

The other site is a bluff overlooking the Red River located on the grounds of the Veteran's Administration Hospital in Shreveport. When we first visited this site in 1977, the area had a number of rare species that were being crowded out by shrubs and vines. Today the shrub layer is cleared yearly in June and July (for non-ecological purposes such as security, snake control, and patient safety), resulting in an environment conducive to *Trillium recurvatum* and *Dentaria laciniata*.

A final point. The negative change recorded here is due entirely to anthropogenic causes: urban sprawl, agroforestry, grazing, farming, and fire suppression. None is the result of natural causes: hurricanes, tornadoes, or river course changes.

CONCLUSION

Over most of the United States, and certainly in environmentally strained Louisiana, we are at a Rubicon in the preservation of our natural heritage. If we continue along the present path, it will be only a matter of time before our native flora is gone. At the present rate of deterioration, our natural heritage soon will exist only as Old Timers' memories and, when they are gone, as inscriptions in the dead black ink on the written page and as exsiccatae in the nation's plant mausoleums.

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NEW COMBINATIONS IN *ODONTADENIA* AND *MANDEVILLA*
(APOCYNACEAE)

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ABSTRACT

New combinations in *Odontadenia* and *Mandevilla* made but not effectively published, in *Checklist of the Plants of the Guianas*, are here validated.

KEY WORDS: Apocynaceae, *Odontadenia*, *Mandevilla*, Flora of the Guianas

In the *Actes de la Société nationale d'Histoire naturelle*, Louis Claude Richard (Rich.) (1792:107) published a catalogue of plants collected in Cayenne by Le Blond, in which he cited four species of *Echites*: *E. biflora* Jacq. = *Rhabdadenia biflora* (Jacq.) Müll.-Arg., as well as three new species accompanied by a Latin diagnosis: *E. puncticulosa*, *E. hirsuta*, and *E. rugellosa*.

Woodson (1933, 1935, 1936) erroneously attributed these species to Achille Richard (A. Rich.), the son of Louis Claude Richard, citing the combinations: *Odontadenia puncticulosa* (A. Rich.) Pulle, *Enum. Vasc. Pl. Surinam*: 383. 1906. and *Mandevilla hirsuta* (A. Rich.) K. Schum., *Engl. & Prantl, Nat. Pflanzenfam.* 4(2):171. 1895. He was unable to identify *Echites rugellosa* A. Rich. (247. 1936.). Woodson was unaware of the handwritten work of Louis Claude Richard, published during the French Revolution, consisting of only a few copies and a single volume and he did not mention the types of Le Blond. In the material studied of the first species, he made no mention of French Guiana, but only Dutch Guiana and Brazil, and did not indicate any types nor did he cite any material from Paris.

For our revision of the Apocynaceae in the Flora of the Guianas, we consulted the Le Blond types in the Lamarck Herbarium (P-LA) as well as the original text of Louis Claude Richard in the Laboratoire de Phanérogamie, which make necessary the following modifications and lectotypifications of these three combinations.

Odontadenia puncticulosa (Rich.) Pulle, *Enum. Vasc. Pl. Surinam*: 383. 1906.
Woodson, *Ann. Missouri Bot. Gard.* 22:285. 1935. BASIONYM: *Echites*

puncticulosa Rich., Act. Soc. Hist. Nat. Paris 1:107. 1792. LECTOTYPE [designated here]: *Le Blond s.n.*, Cayenne, GUYANE. Lectotype: P-LA; Isolectotype: P.

Mandevilla hirsuta (Rich.) K. Schum., Engl. & Prantl, *Nat. Pflanzenfam.* 4(2):171. 1895. Woodson, Ann. Missouri Bot. Gard. 20:762. 1933.; Woodson, Ann. Missouri Bot. Gard. 23:237. 1936. Morales, *Brittonia* 50(2):221. 1998. BASIONYM: *Echites hirsuta* Rich., Act. Soc. Hist. Nat. Paris 1:107. 1792. LECTOTYPE [designated here]: *Le Blond* 387, Cayenne, GUYANE. Lectotype: P-LA; Isolectotype: G-DC.

Mandevilla rugellosa (Rich.) L. Allorge, *comb. nov.* BASIONYM: *Echites rugellosa* Rich., Act. Soc. Hist. Nat. Paris 1:107. 1792. LECTOTYPE [designated here]: *Le Blond* 366, Cayenne, GUYANE. Lectotype: P-LA; Isolectotype: G-DC. *Mandevilla rugellosa* (Rich.) L. Allorge, *comb. inval.*, *Checklist of the Plants of the Guianas*, Boggan J., V. Funk, C. Kelloff, M. Hoff, G. Cremers, & C. Feuillet, 1st edition: 73. December 1992. 2nd: 48. February 1997.

Echites subspicata Vahl, *Elog. Amer.* 2:18. 1798. *Lageguea subspicata* (Vahl) Miers, *Apocyn. S. Amer.* 252. 1878. *Mandevilla subspicata* (Vahl) Markgr., *Rec. Trav. Bot. Neerl.* 22:380. 1926. Woodson, Ann. Missouri Bot. Gard. 20:739. 1933. TYPE: *von Rohr s.n.* (C).

Echites rubricaulis Poirlet, *Encycl. Supp.* 2:535. 1812.; *Tab. Encycl.* 2:314. 1819. Non *Mesechites trifida* (Jacq.) Müll.-Arg. as indicated by Woodson, Ann. Missouri Bot. Gard. 23:247. 1936. TYPE: *L.C. Richard s.n.*, GUYANE. HOLOTYPE: P; Isotype: P-JU. *Syn. nov.*

Echites guianensis A. DC., *Prodr.* 8:458. 1844. *Amblyanthera guianensis* (A. DC.) Müll.-Arg., *Linnaea* 30:448. 1860. *Mesechites guianensis* (A. DC.) Miers, *Apocyn. S. Amer.* 235. 1878. TYPE: *s.n. s. coll.*, Cayenne (G-DEL).

Lasegua venustula Miers, *Apocyn. S. Amer.* 252. 1878. TYPE: *von Rohr s.n.*, Cayenne (BM).

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NOMENCLATURAL AND TAXONOMIC NOTES ON COSTA RICAN PALMS
(ARECACEAE), WITH FIVE NEW SPECIES

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ABSTRACT

Five new species of Arecaceae, all apparently endemic, are described from Costa Rica: *Bactris polystachya* H. Wendl. ex Grayum, *Calyptrogyne herrerae* Grayum, *Chamaedorea hodelii* Grayum, *Geonoma brenesii* Grayum, and *Geonoma talamancana* Grayum. The obscure and much-abused name *Chamaedorea graminifolia* H. Wendl. is applied to a rare Costa Rican species; *Chamaedorea schippii* Burret, based on a Belizean collection, is removed from the synonymy of *C. graminifolia*, and the description of the latter species is amended accordingly. *Chamaedorea coralliformis* Hodel and *C. crucensis* Hodel are shown to be synonymous; *C. crucensis* has priority, and thus becomes the accepted name. The prevailing application of the name *Chamaedorea zamorae* Hodel, to an orange-fruited species of the Pacific lowlands of Costa Rica, is upheld. A key to the Costa Rican and Panamanian species of *Chamaedorea* subgen. *Stephanostachys* with spicate inflorescences is provided. The name *Desmoncus costaricensis* (Kuntze) Burret is interpreted as applying to the rarer of two *Desmoncus* spp. occurring on the Atlantic slope of Costa Rica, and its basionym (*Atitara costaricensis* Kuntze) is epitypified. The name *Desmoncus schippii* Burret is accepted for the second, more common species, and full synonymy is provided. The authorship of the name *Elaeis oleifera* (Kunth) Cortés is retained as such.

KEY WORDS: Arecaceae, *Calyptrogyne*, *Chamaedorea*, *Desmoncus*, *Elaeis*, *Geonoma*, Palmae, Costa Rica, systematics

Work toward a treatment of the palm family (Arecaceae) for Costa Rica has uncovered five species new to science, in four genera. These novelties are here published, for use in several upcoming regional floras. At the same time, several other miscellaneous nomenclatural and taxonomic problems are resolved.

BACTRIS

BACTRIS POLYSTACHYA H. Wendl. ex Grayum, *spec. nov.* TYPE: COSTA RICA. Alajuela: Cantón de Upala, along Río Chimurria in vicinity of Colonia Puntarenas, ca. 11 km (by road) SE of Upala, 10° 49' N, 84° 53' W, ca. 80–100 m, 17 Nov 1988, M.H. Grayum, G. Herrera, & R. Evans 9044 (HOLOTYPE: MO!; Isotype: INB!).

Species cum *Bactride longiseta* H. Wendl. ex Burret optime congruens, sed differt foliis numerosioribus longioribus angustioribusque ordinate dispositis in plano unico setis marginalibus brevioribus.

Stems 3–6 m tall and ca. 2.0–2.5 cm diam., the internodes spiny. Petioles beyond sheath 14–49 cm, unarmed or sparsely spiny. Leaf-blades pinnately compound, to ca. 1.35 m long, the rachis densely brownish scurfy, unarmed or remotely spiny, leaflets 15–31 per side, regularly spaced, arranged in a single plane, 30–83 × 3.5–7.0 cm (medial ones), linear to narrowly elliptical, usually with larger marginal spines ca. 0.4–2.5 cm. Peduncle ca. 10 cm, strongly recurved, with bract 23–37 cm long, densely spiny. Infl. rachis 1.5–5.0 cm; rachillae 20–30, 4.5–11.0 cm long. Male fls. ca. 4–5 mm long. Female fls. ca. 2.5–3.0 mm long; calyx nearly as long as corolla; staminodes not evident. Ripe frts. ca. 1.5–1.8 × 1.5–1.8 cm, oblate to obovoid, bluntly rostrate, orange.

Endemic to Costa Rica, Atlantic slope of the Cordilleras de Guanacaste and Central and adjacent coastal plains; 0–150 m.

ADDITIONAL SPECIMENS EXAMINED. COSTA RICA. Province Unknown: flum. Sarapiquí, *Wendland s.n.*, 1857 (K). Heredia: Boca del Toro Amarillo, Sarapiquí, *Poveda 1017* (CR). Limón: Refugio Nacional de Fauna Silvestre Barra del Colorado, forests and pastures between Río Chirripocito and R. Sardina ("Sardinal" on Chirripó Atlántico quadrangle), 10° 38' N, 83° 45' W, ca. 10–15 m, *Grayum et al.* 8999 (MO).

Bactris polystachya comprises relatively large plants, resembling the coastal *B. major* Jacq. in stature and general aspect (namely, in having pinnately compound leaf-blades with the leaflets regularly spaced and arranged in a single plane). However, it differs sharply from *B. major* in its wider leaflets, shorter peduncles, more congested inflorescences with more numerous, shorter rachillae, absence of a staminodial ring in the corollas of the female flowers, smaller, orange (rather than purplish) ripe fruits, and forest habitat.

The new species is probably most closely related to a small group of Central American species with similar inflorescence structure and fruits, including *Bactris caudata* H. Wendl. ex Burret, *B. grayumii* de Nevers & Andrew Hend., and *B. longiseta* H. Wendl. ex Burret. These species differ from *B. polystachya* in having either simple leaves (*B. grayumii*) or else pinnately compound leaves with the leaflets clustered and arranged in more than one plane. Most similar to *B. polystachya* is *B. longiseta*, which shares prominent spines (to > 1 cm long) along the margins of the

leaflets. Indeed, these two taxa were not distinguished by de Nevers *et al.* (1996), who lumped both under *B. longiseta*. *Bactris polystachya* differs additionally from *B. longiseta* in its more numerous, longer and narrower leaflets with shorter marginal spines. Scattered reports of purplish fruits in *B. longiseta* suggest a more significant possible difference, but need verification.

Bactris polystachya was first collected by German horticulturist Hermann Wendland in 1857, along the Río Sarapiquí (Wendland s.n. [K]). The name "*Bactris polystachya*" is written on the label in Wendland's hand, suggesting that he recognized this as a new species distinct from *B. caudata* and *B. longiseta*, both of which he collected on the same trip and named distinctly. The last-mentioned two names were eventually validated by Burret (1933–1934); but, although the name *Bactris polystachya* has appeared several times in the literature as a *nomen nudum* (Hemsley 1882–1886; Dahlgren 1936; Standley 1937; Henderson *et al.* 1995; de Nevers *et al.* 1996), it has never been published validly.

The Wendland specimen is the only flowering collection of *Bactris polystachya* that I have seen; consequently, all of the inflorescence and floral data in the above description pertain to this specimen. Because Wendland's label does not indicate the month of the collection, no information on flowering phenology is available for this species.

According to the label of *Poveda 1017*, the *palmito* of *Bactris polystachya* is "dulce" and "muy agradable."

CALYPTROGYNE

CALYPTROGYNE HERRERAE Grayum, *spec. nov.* TYPE: COSTA RICA. Limón: Cantón de Limón, N flank of Fila Matama in headwaters of Río Boyei, Cordillera de Talamanca, 9° 45' N, 83° 19' W, 1200–1300 m, 17 Aug 1995. *M.H. Grayum 11043* (HOLOTYPE: INB!; Isotypes: CR!, MO!).

A *Calyptrogyne trichostachyde* Burret petiolis stipite inflorescentiaeque brevioribus et sepalis florum masculinorum glabris margine ciliatisve, a *C. condensata* (L.H. Bailey) Wess. Boer rhachidi inflorescentiae longiore relative gracilioreque et floribus dissitoribus recedit.

Plants subcaulescent. Petioles beyond sheath ca. 11.5–31.0 cm. Leaf-blades pinnately compound, the rachis 62–90 cm, leaflets 10–14 per side, 16–48 cm long (medial ones). Peduncle (to scar) 123–162 cm. Infl. rachis ca. 22–24 cm, densely reddish brown stellate-tomentose (more sparsely so past anthesis); stipe ca. 0.9–2.0 cm long. Male fls. ca. 5.0 mm long, the sepals ± glabrous, or marginally ciliate; anthers ca. 2.0 mm. Female fls. 2.5–3.0 mm long. Ripe frts. described as "lila, dulces" (Herrera 8836), otherwise unknown.

Endemic to Costa Rica, Atlantic slope of Cordillera de Talamanca; 900–1400 m; August.

ADDITIONAL SPECIMENS EXAMINED. COSTA RICA. Limón: filas al este de Almirante, divisoria de aguas entre la cuenca superior de Río Xichiari [sic] y Río Boyei, 9° 44' 20" N, 83° 18' 30" W, 1400 m, *Herrera & Rojas A. 8492* (CR, 3 sheets); [Cantón de] Siquirres, Las Brisas de Pacuarito, siguiendo la fila superior margen izquierda de Quebrada Jesús, camino a Cerro Tigre, 9° 57' 00" N, 83° 25' 50" W, 900 m, *Herrera 8836* (CR).

Calypstrogyne herrerae is known from just three collections, all from mid-elevations on the Atlantic slope of the Cordillera de Talamanca north of Fila Matama. It belongs to a small group of species characterized by having the stipe and rachis of the inflorescence densely reddish-brown-tomentose, rather than glabrous or virtually so. The most well known species in this group is *C. trichostachys* Burret, of northern Costa Rica, which differs from the new species in having longer petioles (25–65 cm), longer inflorescence stipes (3.8–14.0 cm), and male flowers with the sepals densely tomentose distally. Somewhat more similar is *C. condensata* (L.H. Bailey) Wess. Boer, of extreme southeastern Costa Rica and adjacent Panamá at ca. 0–750 m; this differs from *C. herrerae* in having much shorter [9.3–11.8(–13.5?) cm] and relatively stouter inflorescence rachises, with more congested flowers.

It is an honor to dedicate this species to my valued friend and field companion of the last fifteen years, Gerardo Herrera Chacón, of Macacona de Esparza, Costa Rica. Gerardo, responsible for two of the three collections cited above, is widely respected as the most accomplished generalist plant collector currently working in the Mesoamerican region. This will also serve to commemorate his long-sought conquest of Cerro Tigre, which lived up to its promise in yielding this and many other significant records.

CHAMAEDOREA

A good, recent collection has spurred a reinterpretation of the long-misunderstood *Chamaedorea graminifolia* H. Wendl. As a result, a revised and augmented description of this species is here presented:

CHAMAEDOREA GRAMINIFOLIA H. Wendl., *Index Palm.* 62. 1854. TYPE: cult. Hannover (orig. "Guatemala?"), *Wendland s.n.* (HOLOTYPE: GOET!).

Stems solitary, to at least 2.5 m tall and 2.5 cm diam. Lvs. in crown ca. 3–5. Petioles beyond sheath ca. 21–30 cm, with basal, adaxial callus, the sheath tubular for most of its length and forming a brief crownshaft. Leaf-blades pinnately compound, the rachis ca. 66–88 cm; leaflets ca. 32–36 per side, ca. 25–31 × (0.3–)1.1–1.3 cm (medial ones), straight. Infls. infrafoliar; peduncle ca. 34–50 cm, suberect. Male infls. racemously branched; rachis ca. 2–7 cm; rachillae 5–15+, ca. 21–35 cm × 5–6 mm (fresh), pendulous; fls. (fresh) ca. 2–3 mm long, green, the petals distinct,

nerveless. Female infls. (in fruit) racemosely branched; rachis ca. 4.8 cm; rachillae 7, ca. 20–25 cm. Ripe frts. ca. 0.7×0.35 cm, smooth, ellipsoid.

Costa Rica and (perhaps) SE Nicaragua, Atlantic slope, Llanuras de San Carlos to Cordillera de Talamanca (near Panamanian border), 0–650+ m.

ADDITIONAL SPECIMENS EXAMINED. COSTA RICA. [Alajuela:] plains of San Carlos, 100 m, *Cook & Doyle* 78 (US [5 sheets]; photo!); San Carlos, *Th. F. Koschny s.n.* [10] Mar. 1901 (GOET [5 sheets]; photo!). Limón: Finca Montecristo, on the Río Reventazón below Cairo, ca. 25 m, *Standley & Valerio* 49006 (US; photo!).

CULTIVATED. cultivada en el vivero del Sr. G. Herrera, San Miguel de Naranjo [Prov. Alajuela], Costa Rica, semillas traídas del Cerro Nimaso, Talamanca, [Prov.] Limón, $9^{\circ} 28' 6''$ N, $83^{\circ} 02' 4''$ W, 1093 m¹, *Cascante ex Herrera* 1410 (CR).

The name *Chamaedorea graminifolia* is based on a specimen prepared from a staminate plant of questionable origin cultivated in Germany about 150 years ago. Furthermore, the herbarium containing the type was lost for many years, though it was rediscovered about 30 years ago and is extant at GOET (see Wagenitz 1972). Consequently, the correct application of the name has long been in doubt, and it has been applied rather wantonly to a variety of species (as discussed by Hodel 1992).

Hodel (1992) studied most of the specimens cited above, but based his description of *Chamaedorea graminifolia* largely upon material from northern Mesoamerica that had previously been attributed to *C. schippii* Burret (a name newly synonymized by Hodel under *C. graminifolia*). The name *Chamaedorea schippii* is unambiguously typified by a Belizean collection, corresponding to a distinctive species (well known to Hodel in the field) characterized by its unusual, open-cespitose growth habit, with long-spreading rhizomes, pinnately compound leaf-blades with rather numerous, narrow, plicate leaflets, and limestone habitat. The morphology of the male flowers of Belizean material (with nerved petals connate basally and apically) would suggest membership in subgen. *Chamaedorea*, nevertheless, Hodel (1992) included *C. graminifolia* in subgen. *Chamaedoropsis* Oerst., presumably on the basis of the corollas of the male flowers on the holotype collection (reinterpreted by Hodel as apically free, rather than connate, as stated in the protologue).

All of the Costa Rican collections cited above are either sterile or (*Cook & Doyle* 78) fruiting, with the exception of *Cascante ex Herrera* 1410, a staminate collection at full anthesis. My exhaustive analysis of these specimens, in conjunction with the type of *Chamaedorea graminifolia* and material from northern Mesoamerica previously attributed to *C. schippii* (including the type), has led to the following principal conclusions: first, the Costa Rican collections, though from disparate sites and representing both genders, exhibit a fundamental uniformity in all their features, and

¹This is the summit elevation of Cerro Nimaso, as per the specimen label. However, according to Gerardo Herrera (the original collector), the population was located further downslope, perhaps 2/3 of the way toward the summit, hence, the "650+" figure in the foregoing distribution summary.

may be confidently regarded as conspecific; second, the Costa Rican collections do not match the holotype or the original description of *C. schippii*, or any other material from Belize and adjacent countries so identified; third, the Costa Rican collections exhibit a near-perfect congruence, in all critical details, with the type and protologue of *C. graminifolia*, for which they are a better match than *C. schippii* (or any other named entity); fourth, and following automatically from the preceding conclusions, the name *C. schippii* applies to a distinctive species with no other valid name, and should thus be liberated from the synonymy of *C. graminifolia*.

The Costa Rican species here designated as *Chamaedorea graminifolia* differs from the more northern *C. schippii* (and agrees correspondingly with the holotype of *C. graminifolia*, where comparison is possible) in numerous features, including its solitary habit (*Cascante ex Herrera 1410*), narrower (< 1.5 cm) leaflets, longer peduncles, fewer, longer, and thicker male rachillae, staminate floral morphology (with distinct, nerveless petals), fewer and longer female rachillae, and narrower (absolutely and proportionately) fruits. The morphology of the male flowers (as evaluated from both the holotype and *Cascante ex Herrera 1410*) precludes membership in subgen. *Chamaedorea*; instead, *C. graminifolia* must belong either to subgen. *Chamaedoropsis* or (because of its relatively thick, lax, densely flowered male rachillae) subgen. *Stephanostachys* Klotzsch.

Chamaedorea graminifolia is apparently a very rare and local species, and one that has seldom been cultivated. *Cook & Doyle 78*, collected in 1903, remains the only known fertile specimen prepared from a wild-growing plant (as well as the only pistillate collection). The Koschny collection was cited by Burret (1933:740), who had also seen Wendland's original material. Burret's familiarity with this authentic material of *C. graminifolia* lends credence to his citation of a Nicaraguan collection, *Schramm s.n.* (probably at B, and now apparently lost), under that name. The locality of the Schramm collection (Bluefields, in southeastern Nicaragua) is harmonious with the known occurrence of *C. graminifolia* in northeastern Costa Rica. The provenance of *Cascante ex Herrera 1410* suggests that *C. graminifolia* should also be sought in Prov. Bocas del Toro, Panamá. Wendland's (1854) indication of "Guatemala?" as the provenance of his living (type) material should be no cause for consternation, because that name is known to have been used by several early horticultural collectors (e.g., von Friedrichthal) to include Costa Rica.

CHAMAEDOREA HODELII Grayum, *spec. nov.* TYPE: COSTA RICA. Cartago: Cantón de Paraíso, Valle del Reventazón, unión del Río Grande de Orosi y Dos Amigos, 9° 42' 18" N, 83° 47' 02" W, 1480 m, 19 Jul 1994, E. Lépiz, J. González, & J.F. Morales 485 (HOLOTYPE: INB-582382!, INB-582383!).

Differt a *Chamaedorea allenii* L.H. Bailey sepalis florum masculinorum distinctis et fructibus maturis laevibus, a *C. crucensi* Hodel atque *C. zamorae* Hodel petalis florum masculinorum in dimidio inferiore connatis et fructibus maturis atropurpureis.

Stems solitary, 0.7–2.0 m tall and ca. 0.9–2.0 cm wide. Lvs. in crown 3–6. Petioles beyond sheath 6.5–32.0 cm, the sheath split distally, mostly tubular. Leaf-blades pinnately compound, the rachis 14.5–54.0 cm; leaflets 7–10 per side,

(10–)14–34 × 1.7–7.6 cm (medial ones), sigmoid. Infls. interfoliar (becoming infrafoliar); peduncle 17.5–46.0 cm, suberect to nodding. Male infls. spicate; rachis ca. 20–22 cm, pendulous; fls. ca. 6.5–7.0 mm long, light green to yellow, the petals connate for 1/2–3/4+ their length and erect distally, lightly nerved. Female infls. spicate; rachis ca. (3.3–)7.0–11.5(–17.5) cm, suberect to nodding; fls. ca. 2–3 mm long, greenish white. Ripe frts. 1.0–1.1 × 0.8–1.0 cm, smooth, subglobose or obovoid-prismatic, dark purple or black.

Endemic to Costa Rica, Atlantic slope and near Continental Divide, Cordilleras de Tilarán (rare), Central, and Talamanca; (700–)1100–2000+ m; May, July–November.

ADDITIONAL SPECIMENS EXAMINED. COSTA RICA. Alajuela: Monteverde, Reserva Biológica Monteverde, 5 km NW of Poco Sol, 10° 23' N, 84° 42' W, 1300 m, *Ivey 97* (CR [3 sheets]). Cartago: about 15 km S of Tapantí, on the E slope above the Río Grande de Orosi, 9° 42' N, 83° 47' W, 1500 m, *Burger & Liesner 6829* (CR); Tapantí, 1300–1700 m, *I.A. Chacón et al. 1427* (CR,MO); cañón del Río Grande de Orosi y aluvión, *I.A. Chacón et al. 1492* (CR [2 sheets],MO); Tapantí Reserve, ca. 1 km S of jct. of Quebrada Salto and Río Grande de Orosi, along trail heading eastward into mountains, 9° 43' N, 83° 47' W, 1500–1800 m, *Croat & Grayum 68283* (MO); Reserva de Tapantí, 1300–1800 m, *Gómez 18790* (MO), *18868* (MO), *18881* (MO); Tapantí, 1400–1700 m, *Gómez 19206* (MO); [Cantón de] Turrialba, Cerro Tigre, cabeceras de quebradas innominadas, cuenca superior de Quebrada Ayil, 9° 55' 10" N, 83° 23' 25" W, 1200 m, *Herrera & Mora 8910* (CR); [Cantón de] Turrialba, Cerro Tigre, siguiendo la quebrada innominada, bajando hasta Lago Ayil, 9° 54' 40" N, 83° 22' 55" W, 700 m, *Herrera & Valverde 8924* (CR); Cantón de Turrialba, 6 km beyond Moravia at crossing of Río Platanillo, 9° 49' 10" N, 83° 33' 00" W, 1000–1500 m, *Hodel & Grayum 982* (CR); lower slopes of Alto Patillos, 6.5 km SE of Tapantí, 1470 m, *Lent 1080* (CR [3 sheets]); Cantón de Paraíso, unión del Río Grande de Orosi y Dos Amigos, 9° 42' 18" N, 83° 47' 02" W, 1480 m, *Lépiz et al. 483* (CR,INB); ca. 6 km S of Cartago by air, Quebrada Cangreja, 3 km S of Pan American Highway, remnant forest, 9° 46' N, 83° 57' W, 1620–1650 m, *Liesner & Judziewicz 14497* (CR,MO); P. N. Tapantí, sector Quebrada Segunda, 9° 45' 50" N, 83° 47' 15" W, 1200–1400 m, *Mora 317* (INB); Reserva Forestal Tapantí, Sendero Oropéndola, 9° 54' 06" N, 83° 47' 27" W, 1300 m, *J.F. Morales et al. 421* (CR [2 sheets]); vicinity of Orosi, *Standley 39923* (US); El Muñeco, on the Río Navarro, 1400–1500 m, *Standley & Torres R. 51700* (US); cerca del Mirador, Tapantí, ± 1200 m, *Umaña et al. 370* (CR); Orosi, Refugio de Fauna Silvestre, Tapantí, Sendero Palmito, *Marlon Valerio et al. 27* (CR). Heredia: Parque Nacional Braulio Carrillo, 10° 15' N, 84° 06' W, 1450 m, *Chazdon 187* (CR); Parque Nacional Braulio Carrillo, 11 km S, 11.5 km E of San Miguel, 10° 16' N, 84° 05' W, 1130 m, *Chazdon 204* (CR [2 sheets]); Cerro de Las Caricias, north of San Isidro, 2000–2400 m, *Standley & Valerio 52452* (US). Limón: Cantón de Limón, N flank of Fila de Matama in headwaters of Río Boyei, Cordillera de Talamanca, 9° 45' N, 83° 19' W,

1200–1300 m, *Grayum 11012* (INB); Cantón de Guápiles, Los Angeles, San Miguel, siguiendo el camino entre Río Blanco y Río Blanquito, 10° 06' 20" N, 83° 50' 40" W, 1200 m, *Herrera 3759* (CR); Cordillera de Talamanca, sendero de Quebrada Kuisa a Río Lori, entre Ujarrás y San José Cabécar, 9° 21' 30" N, 83° 14' 00" W, 1780 m, *Herrera 5925* (INB), [Cantón de] Limón, filas al este de Almirante, cuenca superior Río Boyei, rumbo a Fila Matama, 9° 44' 20" N, 83° 17' 40" W, 1300 m, *Herrera 8510* (CR); Cantón de Limón, El Progreso, Fila Matama, 9° 47' 18" N, 83° 08' 45" W, 1350 m, *Herrera & Chacón 2666* (CR). Puntarenas: [Cantón de] Puntarenas, La Pitahaya, Rincón, siguiendo la fila entre Río Aranjuez y Quebrada Vueltas, 10° 15' 30" N, 84° 41' 00" W, 1400 m, *Herrera et al. 9086* (CR). San José: south facing slopes of Cerro Zurquí at termination of Calle Zurquí ["San José/Heredia Province Border"], 1800–2000 m, *Almeda & Nakai 3705* (CR); Parque Nacional Braulio Carrillo, La Montura, 900–1100 m, *Chazdon 237* (BH [3 sheets]), *Hodel et al. 977* (BH, CR); Bajo de Hondura, Parque Nacional Braulio Carrillo, ca. 10° 4' N, 83° 58' W, 1100–1200 m, *Davidse et al. 23159* (MO); Alto La Palma, 1500 m, *Gómez 4039* (CR [4 sheets]); Braulio Carrillo, area Zurquí ["Prov. Heredia"], 1800 m, *Gómez 20093* (MO), *20095* (MO); eastern spur ridge of Cerro Hondura, between Río Patria and Río Zurquí (north of tunnel), Cordillera Central, 10° 04' N, 84° 01' W, 1500–1600 m, *Grayum & Sleeper 6123* (MO); Parque Nac. Braulio Carrillo, trail from hwy. at La Ventana to Bajo La Hondura, 10° 04' N, 83° 59' W, 1100–1300 m, *Solomon 19178* (INB).

Chamaedorea hodelii is a member of subgen. *Stephanostachys*, an essentially Mesoamerican group of about ten species characterized by more or less lax, densely flowered staminate inflorescences. This is a moderately well-known species of montane Costa Rica, adequately represented in herbaria for the better part of the century. However, these collections have been filed under a confusing succession of names, reflecting the gradual evolution in our understanding of the taxonomically complex group to which this species belongs. Now that the dust may have finally settled, it appears that this familiar species has somehow been left with no name at all!

Standley (1937) applied the name *Chamaedorea arenbergiana* H. Wendl. to material primarily or exclusively representing *C. hodelii*. Subsequently, the name *Chamaedorea allenii* L.H. Bailey was much employed (in herb.), in a broad sense, to most of the Costa Rican species of subgen. *Stephanostachys* with spicate inflorescences (especially, to *C. hodelii*, *C. crucensis* Hodel, and *C. zamorae* Hodel). However, as shown by Hodel (1990, 1992), *Chamaedorea arenbergiana* is a more northern species (southern México to Honduras), larger than *C. hodelii* in all its vegetative parts, with shorter peduncles and racemosely branched male inflorescences (with 8–10 rachillae), while *C. allenii* is a more southern species (west-central Panamá to northwestern Colombia), characterized by bright yellow male fls. with fully connate sepals and finely echinulate ripe frts. Most recently, the material here assigned to *Chamaedorea hodelii* has been subsumed (in herb. and by Hodel 1992) within *C. crucensis*, of similar elevations on the Pacific slope of Costa Rica; however, the latter species (as here interpreted) is well distinguished by having larger leaves with more numerous (6–13) leaflets, staminate flowers with more or less distinct petals, and bright orange to red, verrucose-echinulate ripe fruits.

The recognition here of *Chamaedorea hodelii* as a distinct, previously unnamed species is the result of an investigation into the identity of *C. crucensis*, which itself requires some explanation. The type of the latter name, and all of the original material, was collected from remnant forests adjacent to the Las Cruces Botanical Garden (now Jardín Botánico Robert y Catherine Wilson) in extreme southwestern Costa Rica (Hodel 1990). Later, Hodel (1992) enlarged the concept of *C. crucensis* by including numerous collections from montane regions of central Costa Rica. Some of this last-mentioned material, here distinguished as *C. hodelii*, is illustrated under the name *Chamaedorea crucensis* in Hodel (1992: Plate 115B–E).

I soon began to suspect, on morphological grounds, that two different species were mixed under the name *Chamaedorea crucensis*. The material from central Costa Rica appeared to differ consistently from all of the collections I had seen from the Las Cruces region, particularly in leaf dimensions and leaflet number. Indeed, the Las Cruces population, upon which the name *C. crucensis* was typified, emerged as poorly understood in general, with respect to the other, comparatively well-circumscribed Costa Rican entities in this complex. None of the wild collections I had seen from Las Cruces bore either staminate inflorescences or ripe fruits, both crucial for species identification in this complex. Based on phytogeographic precedent, the Las Cruces forests might reasonably be expected to harbor any of several species in this group, including the more upland *C. coralliformis* Hodel (1996), the more lowland *C. zamorae*, the more southern *C. allenii*, the mainly Atlantic slope species here called *C. hodelii*, or even a very local endemic; moreover, many non-indigenous species are cultivated at the site, and the provenance of herbarium collections (*i.e.*, forest or garden) is not always indicated clearly on labels (and may be ambiguous even in the field). The challenge thus shifted to establishing the correct application of the name *C. crucensis* according to its type. This difficulty was exacerbated by the fact that I had not (and still have not) been able to locate either the holotype (Hodel & Hodel 706A) or the single isotype of *C. crucensis*, ostensibly at BH and CR, respectively, but not currently present at either institution.

I approached this problem by generating rigorous, specimen-based descriptions of all the taxonomic entities involved, as I understood them, with special attention to the seldom collected, yet diagnostically critical, staminate inflorescences. These descriptions were then compared with a parallel description of wild-collected Las Cruces material, augmented considerably by a recent loan from BH which contained both staminate inflorescences and virtually ripe fruits. My conclusion is that the indigenous Las Cruces population corresponds unequivocally and exclusively to the species known previously as *Chamaedorea coralliformis*, which name thus becomes a synonym of the earlier *C. crucensis*.

The distinct petals and sepals of male flowers of the two wild-collected staminate Las Cruces collections, Moore & Parthasarathy 9444 (BH) and Read 651 (BH), immediately eliminate *C. hodelii* and *C. allenii*, the male flowers of which have connate petals and sepals, respectively. The male flowers of both Las Cruces collections have narrowly ligulate sepals nearly as long as the petals, just as in *C. coralliformis*, but not *C. zamorae* (with quadrate or obdeltate sepals about half as long as the petals). The staminate sepals are also described as "narrow" in the protologue of *C. crucensis* (Hodel 1990). Fruits of Las Cruces collections are described as "orange-red" [on Moore & Parthasarathy 9431 (BH), where they are not present] and

"maturing red" [on Moore 9991 (BH), where they are present], in agreement with *C. coralliformis* and *C. zamorae*, but not *C. hodelii* or *C. allenii* (which have black fruits). Some fruits on Moore & Parthasarathy 9444 (BH) clearly exhibit evidence of the echinulae characteristic of *C. coralliformis*, but not of *C. zamorae*. Finally, leaflet number in the Las Cruces population ranges from 7–13 per side, as typical only of *C. coralliformis* (none of the other species mentioned in this paragraph is known to have more than 10 leaflets per side).

Because the type collection of *Chamaedorea coralliformis* (Hodel & Binder 1345 [BH!]) is pistillate, information on staminate inflorescences was obtained from specimens collected in the region of the type locality, in association with pistillate material, and agreeing with the latter in vegetative morphology, e.g., Gamboa *et al.* 26 (INB).

Incidentally, this research has also confirmed the prevailing application of the name *Chamaedorea zamorae*. That name was based, quite unfortunately, on a collection prepared from a plant of somewhat dubious provenance cultivated in Hawaii (Hodel 1990). Although Hodel (1990, 1992) first applied the name to a varied assemblage of material (probably including *C. hodelii*), it has since come to be restricted (in herb. CR,MO,INB) to a distinctive entity, characterized by simple or pinnately compound leaf-blades and bright orange ripe fruits, ranging south from the Reserva Biológica Carara through the Pacific lowlands of Costa Rica. The flowers of the (fortunately!) staminate holotype of *C. zamorae* (Hodel & Bornhorst 830 [BH!]) correspond in all details (as described above) with male flowers of the Pacific lowland entity. The provenance of the type material, indicated as "near Laguna de Arenal, Guanacaste, Costa Rica," must thus be regarded with suspicion, since *C. zamorae* has never been found anywhere near that locale.

Another bothersome, cultivated collection of *Chamaedorea zamorae* is N.W. Uhl s.n. 2 Apr. 1984 (BH), prepared from a staminate plant grown at BH (as BH76:620) from seeds obtained by H.E. Moore, Jr. from Las Cruces. This specimen can be identified unambiguously as *C. zamorae* on the basis of its simple leaf-blades (unknown in *C. coralliformis*/*C. crucensis*), as well as its floral morphology. Although these seeds probably came from non-indigenous material cultivated at Las Cruces, it is possible that *C. zamorae* may also (*i.e.*, in addition to *C. crucensis*) occur naturally in the vicinity.

Chamaedorea hodelii, here denoting the material from central montane Costa Rica included by Hodel (1992) in *C. crucensis*, differs substantially from the latter species in having shorter petioles with mostly tubular sheaths, shorter leaf-blades with fewer and more strongly sigmoid leaflets, longer male flowers with the petals connate for half or more their length, and smooth, purplish to black fruits. The distinctions among the various species discussed in the foregoing paragraphs are summarized in the following key, which treats all Costa Rican and Panamanian members of subgen. *Stephanostachys* with spicate (or, rarely, furcate) inflorescences. Note that the key includes *Chamaedorea robertii* Hodel & N.W. Uhl, assigned by Hodel (1992) to subgen. *Chamaedoropsis* but, in my view, better accommodated here.

- 1 Leaf-blades all simple, bifid.
 - 2 Plants often acaulescent at maturity (always so in Costa Rica); leaf-blades with ca. 9–16 primary lateral veins per side; peduncular bracts of female inflorescences purplish; ripe fruits black, smooth; Atlantic slope. *C. robertii*
 - 2' Plants usually caulescent at maturity (*C. allenii* may be acaulescent); leaf-blades with ca. (11–)15–50 primary lateral veins per side; peduncular bracts of female inflorescences green; ripe fruits orange or (if black) echinulate; both slopes.
 - 3 Male inflorescences multiple (ca. 4–10) per node, the rachises ca. 5.5–9.5 cm; ripe fruits orange to red-orange, smooth; Atlantic slope. . *C. deckeriana*
 - 3' Male inflorescence solitary at nodes, the rachises ca. 10–27 cm; ripe fruits orange or black, smooth or echinulate (if orange and smooth, plants of Pacific slope).
 - 4 Sepals of male flowers connate in a ring; ripe fruits black, echinulate; Panamá and NW Colombia. *C. allenii*
 - 4' Sepals of male flowers distinct; ripe fruits orange to orange-red, smooth; Costa Rica. *C. zamorae*
- 1' Leaf-blades (at least some) pinnately compound.
 - 5 Sepals of male flowers connate in a ring; ripe fruits blackish, echinulate; Panamá and NW Colombia. *C. allenii*
 - 5' Sepals of male flowers distinct; ripe fruits orange to red, or (if blackish) smooth; Costa Rica.
 - 6 Petals of male flowers connate for more than half their length; ripe fruits black; Atlantic slope and near Continental Divide. *C. hodelii*
 - 6' Petals of male flowers distinct; ripe fruits orange to red; Pacific slope.
 - 7 Leaflets ca. 6–13 per side; sepals of male flowers narrowly ligulate to oblanceolate, > 2× as long as wide, ca. 3/4 to as long as petals; ripe fruits coarsely echinulate; (1150–)1500–2300 m. *C. crucensis* (including *C. coralliformis*).
 - 7' Leaflets ca. 3–9 per side; sepals of male flowers quadrate to obdeltate, ca. 1–2× as long as wide, ca. 1/2 as long as petals; ripe fruits smooth; 50–500(–800) m. *C. zamorae*

It gives me great pleasure to dedicate this new species to my friend and colleague Donald R. Hodel, of the University of California at Los Angeles, who, in ten short years, has created order out of chaos in *Chamaedorea*.

DESMONCUS

The genus *Desmoncus* is notoriously difficult taxonomically. In Costa Rica, it is represented by at least three species: the highly distinctive, non-scandent *Desmoncus stans* Grayum & de Nevers (1988), of the southern Pacific lowlands, and two scandent species of the Atlantic lowlands. Scattered collections of scandent

Desmoncus from the Pacific slope may represent as many as two additional species, but this material is inadequate for determination and cannot be dealt with here.

The two well-characterized, scandent *Desmoncus* species of the Costa Rican Atlantic lowlands are distinguished as follows:

- 1 Weakly scandent plants in understory, to ca. 2.5–6.0 m tall; petiole beyond sheath ca. 10–16 cm; foliar leaflets (*i.e.*, excluding acanthophylls) ca. 8–11 per side, broadly elliptical, the larger ones > 5 cm wide, spineless adaxially; inflorescence rachis ca. 4.5–5.5 cm; rachillae ca. 15–17, ca. 3–7 cm; 0–200+ m, Atlantic slope Cordillera de Talamanca..... *Desmoncus* sp. I
- 1' Robust lianas often ascending to canopy, fertile individuals ca. 5–20+ m tall; petiole beyond sheath ca. 1.5–5.0 cm; foliar leaflets ca. 16–23 per side, narrowly elliptical to lanceolate, the larger ones < 5 cm wide, with beard of spines adaxially at base; inflorescence rachis ca. 12–24 cm; rachillae ca. 19–44, ca. 4.5–21.0 cm; 0–300 (–600) m, N Atlantic slope (Llanura de Guatuso to Llanura de Tortuguero)..... *Desmoncus* sp. II

The correct application of names to these two species has presented a significant challenge. Traditionally, the name *Desmoncus costaricensis* (Kuntze) Burret has been used for any *Desmoncus* collected in Costa Rica. However, for the purpose of producing their field guide in a timely fashion, Henderson *et al.* (1995) synonymized this and all other names for scandent Mesoamerican *Desmoncus* under *D. orthacanthos* Mart., typified by a collection from Atlantic Brazil. This would appear to be a clear case of overlumping, inasmuch as several distinctive scandent *Desmoncus* species occur in the Mesoamerican region. Moreover, the application of the name *D. orthacanthos* to any Mesoamerican entity seems unlikely on biogeographic grounds, and is not supported by morphological evidence (based on my studies of a photo of the type, and of herbarium collections from near the type locality).

With the name *Desmoncus orthacanthos* thus eliminated, the case of *D. costaricensis* must next be considered. Because the latter name pertains to a scandent plant collected in Costa Rica, it almost certainly applies to one of the two species keyed above (even if it is not the earliest name). But despite the distinctiveness of these two species, the identity of *D. costaricensis* is not obvious, even though its basionym (*Aritara costaricensis* Kuntze) is typified by an extant collection (Kuntze *s.n.*, Jun. 1874 [NY]). The holotype looks as though it had been snatched from a passing train: a mangled, moldy, sterile specimen, comprising only the extreme distal portions of two leaf-blades. The citation of the type locality ("südlich von San José im Gebirge") is vague, virtually to the point of inscrutability. No species of *Desmoncus* are known from the mountains immediately to the south of San José (Cerro de la Carpintera, Altos de Tablazo, Cerros de Escazú, *etc.*), and Kuntze's rather hurried traverse through the central part of the country would not have permitted a side-trip to the southern Pacific lowlands. In any case, the date of the collection would nearly guarantee an Atlantic slope site, according to the itinerary of Kuntze (1881:94–115), who entered Costa Rica at Puerto Limón and, by 30 June, had just reached Alajuela.

The published descriptions and holotype of *Desmoncus costaricensis* afford very few clues as to its identity. Two of the better ones must, unfortunately, be discounted.

First, as noted by Burret (1934, in translation²): "The pinnae [of *D. costaricensis*] are broadly lanceolate, in contrast to *D. Schippii* and *D. leiorhachis*." The leaflets of *Atitara costaricensis* are described in the protologue (Kuntze 1891) as "late lanceolata," with the width/length ratio given as "1:4-5." This accords well with *Desmoncus* sp. I, but not sp. II, which generally has much narrower leaflets (ca. 1:9-10+). However, the source of the information on *Desmoncus* (*Atitara*) *costaricensis* is suspect; the holotype presently bears not a single, intact leaflet that would permit the necessary measurements to be made. Moreover, reduced, distal leaflets of sp. II may sometimes be proportionately as broad as the larger leaflets of sp. I, and the holotype of *A. costaricensis* bears only such distal leaflets. Second, the leaflets on the holotype of *A. costaricensis* show no evidence of a basal, adaxial beard of spines, again suggesting sp. I rather than sp. II. But these spines are not evident on every leaf section of sp. II.

Two other morphological details point more convincingly in the direction of sp. I. First, the only leaflet fragment on the holotype of *Atitara costaricensis* that affords a clean width measurement yields a value of ca. 4.2 cm, along an obviously subterminal transect. This is the maximal leaf width I have recorded for the largest leaflets of sp. II; however, because this measurement was taken from one of the smaller (distal) leaflets, and not even at the widest (medial) part, sp. I is strongly implicated. Second, one leaf-rachis on the holotype of *A. costaricensis* bears a stout, black spine ca. 3.1 cm long. This is characteristic of sp. I, but exceeds by nearly 1 cm the maximal leaf-rachis spine length I have recorded for sp. II.

Based on the foregoing rationale, I propose to apply the name *Desmoncus costaricensis* to the species designated as "sp. I" in the above key. I believe the evidence for this to be the best obtainable at the present time. Furthermore, I have found no other name that seems to apply to this species. Because the holotype of *Atitara costaricensis* is scarcely (and arguably) identifiable, and no isotypes exist, I here designate a good, modern collection as epitype (see Art. 9.7 in Greuter *et al.*, 1994):

DESMONCUS COSTARICENSIS (Kuntze) Burret, Repert. Spec. Nov. Regni Veg. 36:202. 1934. BASIONYM: *Atitara costaricensis* Kuntze, Revis. Gen. Pl. 2:726. 1891. TYPE: COSTA RICA. [Province Unknown:] "südlich von San José im Gebirge," Jun 1874, O. Kuntze s. n. (HOLOTYPE: NY!). EPITYPE [here designated]: COSTA RICA. Limón: ridge separating Quebrada Cañabral from Río Barbilla, and slope leading down to the latter, Cordillera de Talamanca, 10° 02' N, 83° 26' W, ca. 200-400 m, 4 Sep 1988, M.H. Grayum, G. Herrera, & R. Robles 8746 (MO!; Isoepitype: INB!).

Desmoncus costaricensis appears to be a local endemic, probably ranging onto the Atlantic slope of western Panamá. However, I have seen no collections from outside Costa Rica. Although the original type locality of *D. costaricensis* is obscure, limited speculation is possible. Kuntze entered Costa Rica at Puerto Limón and traveled directly to San José via Siquirres (Kuntze 1881), very near to the epitype locality cited above. Although Siquirres lies due east (rather than south) of San José, it seems likely

²Original German: "Die Fiedern sind breit lanzettlich, im Gegensatz zu *D. Schippii* und *D. leiorhachis*."

that Kuntze, in the midst of a journey around the world, might not have given much thought to this detail (especially considering the abject condition of his type collection). The reference to "Gebirge" (mountains) may also be significant. According to Kuntze (1881:103), "Von Baguar an beginnt das Gebirge." This would seem to restrict the type locality of *Atitara costaricensis* to the region between "Baguar" (probably a corruption of "Pacuaire," a site just east of Siquirres) and the upward limit of *Desmoncus* habitat along the railway route to the Meseta Central.

Desmoncus sp. II, according to my taxonomic concept, ranges more widely than *D. costaricensis*: north on the Atlantic slope at least to Belize and Guatemala, and conceivably at scattered localities on the Pacific slope of Costa Rica. Because of the adaxial, basal beard of spines on its leaflets, sp. II belongs to the "alliance" of *Desmoncus chinantlensis* Liebm. ex Mart., as circumscribed by Bartlett (1935). Except for *D. costaricensis* and *D. stans* (discussed above), most if not all of the validly published *Desmoncus* names based on Mesoamerican types appear referable to this "alliance." Based on my study of type specimens and original descriptions, I have concluded that several of these names are applicable to sp. II. The oldest of these are *Desmoncus leiorrhachis* Burret and *D. schippii* Burret, based on collections from the same locality in southern Belize. Although I have seen neither type, both protologues are in substantial overall agreement with *Desmoncus* sp. II; moreover, all *Desmoncus* specimens I have seen from southern Belize represent sp. II, in my judgment. Leaf spininess, the principal character employed by Burret (1934) to separate *D. leiorrhachis* (spineless) from *D. schippii* (spiny), is probably inconsequential. I have made collections of both spiny and spineless plants of sp. II at the Estación Biológica La Selva, in Costa Rica (Grayum 7663, 7664 [INB,MO]), and have often observed this sort of variation in species of *Desmoncus* and of other spiny palm genera (e.g., *Bactris hondurensis* Standl.). Moreover, Burret (1934) himself cited a parallel example in a Mexican *Desmoncus*, and acknowledged considerable doubt as to the validity of his *D. leiorrhachis*, suggesting that it might better be treated as a variety of *D. schippii*.

The names *Desmoncus leiorrhachis* and *D. schippii* have equal priority, having been published in the same paper (Burret 1934). I choose the latter as the accepted name, primarily because Glassman (1972) indicated that its type specimen was extant at B, while questioning the existence of a type for *D. leiorrhachis*. Also, as mentioned above, Burret viewed *D. leiorrhachis* as a possible variety of *D. schippii*, not the other way around. My action would appear to establish a formal precedent in preferring one name over the other.

A potential thorn in this scenario is *Desmoncus leptochaete* Burret (1934), based on a Costa Rican type and equal in priority to *D. schippii*. The name *D. leptochaete* has been generally ignored, presumably because (as typical of Burret names) the type is lost and the protologue features no illustration. This name pertains to a scandent species of the Pacific lowlands, the type locality ("Río Abrojo") being near Ciudad Neily, Prov. Puntarenas, in the Golfo Dulce region. The original description of *D. leptochaete* categorically rules out *Desmoncus costaricensis* (sp. I), but concords generally with *D. schippii* (sp. II), although the leaflets are said to lack an adaxial beard of spines. However, I have seen no collections from the Pacific slope unequivocally referable to *Desmoncus* sp. II. Even more perplexingly, the lone fertile collection of a scandent *Desmoncus* that I have seen from the Golfo Dulce region (Aguilar 290 [INB,MO]) matches neither the description of *D. leptochaete*, nor either of the two Atlantic slope species. Thus, I am unable to resolve the identity of *D.*

leptochaete based on the evidence presently available. Should *D. leptochaete* prove conspecific with *D. schippii*, I would hope that some future worker will have the good sense to subordinate the former name.

The complete synonymy of *Desmoncus schippii*, according to my taxonomic concept, is as follows:

DESMONCUS SCHIPPII Burret, Repert. Spec. Nov. Regni Veg. 36:202. 1934.

Desmoncus leiorhachis Burret, Repert. Spec. Nov. Regni Veg. 36:203. 1934.

Desmoncus ferox Bartlett, J. Wash. Acad. Sci. 25:87. 1935.

Desmoncus lundellii Bartlett, J. Wash. Acad. Sci. 25:84. 1935.

Desmoncus quasillarius Bartlett, J. Wash. Acad. Sci. 25:85. 1935.

Desmoncus uaxactunensis Bartlett, J. Wash. Acad. Sci. 25:86. 1935.

I have studied the types of all the Bartlett names cited above. Apart from *Desmoncus leptochaete*, discussed previously, the only regional names for members of the *D. chinantlensis* "alliance" not accounted for in the above synonymy are *D. anomalus* Bartlett, of Guatemala, *D. chinantlensis*, of southern México, and *D. isthmius* L.H. Bailey, of eastern Panamá. *Desmoncus chinantlensis*, in fact, substantially predates *D. schippii*, but I tentatively regard it as applying to a distinct species, based on the morphological evidence adduced by Bartlett (1935). *Desmoncus schippii* predates both *D. anomalus* and *D. isthmius*; the latter clearly pertains to a different species, and I have not seen the type of the former. The *Desmoncus chinantlensis* "alliance" ranges sparingly into South America, but none of the South American collections at MO matches *D. schippii*.

ELAEIS

ELAEIS OLEIFERA (Kunth) Cortés, *Flora de Colombia* 1:203. 1897. BASIONYM:

Alfonsia oleifera Kunth, in Humb., Bonpl. & Kunth, *Nov. Gen. Sp. Quarto ed.* 1:307, *Folio ed.* 1:246. 1816.

The combination *Elaeis oleifera* has long been attributed to Cortés (1897), as indicated above. However, Pires (1995) has recently argued that Cortés, who organized his work on the basis of common names, had no intention of making a new combination, and did not formally do so. Instead, Pires assigned authorship to the next worker to have taken up the name, Wessels Boer (in Lanjouw 1965:144), who fulfilled all the necessary requirements for validating the combination himself, even while crediting it to Cortés.

Although the primary entries in Cortés' work were indeed alphabetized according to common names, he did provide Latin names as well. "Corozo," the main entry in this case, was clearly intended as a common name (it is also a generic name), as pointed out by Pires; however, it is followed by "*Alfonsia oleifera*. HBK.," then by "Elaeis." Under the prevailing *Code* (Greuter *et al.* 1994), the only requirement for

valid publication of new combinations in 1897 would appear to be Art. 33.1, *i.e.*, that "the author definitely associates the final epithet with the name of the genus or species, or with its abbreviation." If that requirement is not met in the *Alfonsia oleifera* entry, it is surely satisfied in the very next one, in which the name "*Martinezia caryotifolia*" is followed immediately by "*Elaeis oleifera*?" This establishes that Cortés did intend to treat *Alfonsia oleifera*, formally or otherwise, under the genus name *Elaeis*. In any case, virtually no formalities are imposed upon new combinations published during Cortés' era, and the question of intent is quite irrelevant; after all, it might equally be argued that Wessels Boer did not intend to be making a new combination.

I therefore reject Pires's argument, and retain Cortés as the extraparenthetical author of the combination *Elaeis oleifera*.

GEONOMA

Study of Costa Rican collections previously determined as *Geonoma cuneata* H. Wendl. ex Spruce, *G. gracilis* H. Wendl. ex Spruce, and *G. jussieuana* Mart. has uncovered two new and apparently endemic species:

GEONOMA BRENESII Grayum, *spec. nov.* TYPE: COSTA RICA. Alajuela: Reserva Biológica de San Ramón, road from Las Lagunas to Colonia Palmareña, 10° 4' N, 84° 32' W, 850–1100 m, 30 May 1986, *G. de Nevers, B. Hammel, & C. Gómez* 7789 (HOLOTYPE: MO-3387522!; Isotype: CR!).

A *Geonoma paradoxa* Burret bractea pedunculari altius affixa et rhachidi inflorescentiae trichomatibus albidis stellatisque vestita, a *G. hugonis* Grayum & de Nevers habitu acaulescenti laminis foliorum pinnatim divisus et bractea pedunculari in prophylo inclusa recedit.

Stems solitary, obsolete to ca. 0.5 m tall and to at least 3 cm diam. Petioles beyond sheath ca. 14–53 cm. Leaf-blades pinnately compound, the rachis 11.0–30.5 cm, leaflets 2–5(–7) per side, ca. 19–37 cm long (medial ones). Infls. interfoliar, spicate; peduncle 16.0–39.5(–56.0) cm, with narrow bract ca. (1.5–)4.2–15.5 cm long (or rarely obsolete), enclosed by prophyll and inserted ca. (0.8–)3.3–11.0(–16.5+) cm above it; rachis 6–19 × 0.2–0.5 cm, ± densely pubescent at anthesis with whitish, mostly branched or stellate hairs with ± flattened arms (later glabrescent). Male fls. ca. 3.0 mm long; stamens 6, the anthers sharply reflexed. Female fls. ca. 3.0–4.0 mm long; staminodial tube deeply crenately to subdigitately lobed. Ripe frts. ca. 0.7–0.8 × 0.5–0.6 cm, striate, broadly ellipsoid to obovoid, black.

Endemic to Costa Rica, Atlantic slope and near Continental Divide, Cordilleras de Tilarán and (very rare) Central; (850?–)1000–1600 m; January–July, October.

ADDITIONAL SPECIMENS EXAMINED. COSTA RICA. Alajuela: UCR Reserva, Fila Volcán Muerte [sic], above the headwaters of the Río San Lorenzo, 10° 12' N, 84° 32' W, 1000–1300 m, *Barringer & Gómez-Laurito 2541* (F); Reserva Biológica Monteverde, Bosque Eterno de los Niños, Quebrada Agua Gata, 10° 20' N, 84° 42' W, 1100 m, *Bello 1808* (CR); La Balsa, San Ramón, *Bermúdez MB245* (USJ); Piedades de San Ramón, 1120 m, *Brenes 4473* (F); Los Angeles de San Ramón, *Brenes 13588* (F [2 sheets]); Reserva de San Ramón, Río San Lorencito, 800–1000 m, *I.A. Chacón 1927* (CR); Reserva Biológica Monteverde, 3 km NW of Poco Sol, 10° 23' N, 84° 41' W, 1050 m, *Ivey 109* (CR); Bosque Eterno de los Niños, near Laguna Poco Sol, 10° 21' N, 84° 41' W, *Ivey 305* (CR). Guanacaste: ca. 3.5 miles from Santa Elena–Monteverde junction near the east edge of Monteverde reserve, ca. 1350 m, *Croat 47118* (MO); 1 km N of Las Nubes on road to Tilarán, 10° 23' N, 84° 51' W, 1200 m, *Ivey 68* (CR); vicinity of Santa Elena, 1500 m, *Meerow et al. 1088* (MO); San Luis de Zarcero, 1550 m, *A. Smith H774* (F [3 sheets]). Puntarenas: Monte Verde, *Bermúdez 144* (USJ [2 sheets]); about 2 km SE of Monteverde, 10° 18' N, 84° 48' W, 1500–1550 m, *Burger & Gentry, Jr. 8563* (CR,F); Monteverde, arriba de Quebrada Cuecha, 1540–1620 m, *Dryer 105* (CR), 872 (CR); Cantón de Puntarenas, Finca Buen Amigo, San Luis, Monteverde, 10° 16' 20" N, 84° 49' 30" W, 1100 m, *Z. Fuentes et al. 218* (INB); Monteverde Preserve, River trail ["Guanacaste"], *Gargiullo 562* (CR); Monteverde, La Torre, 1600 m, *Haber & Bello C. 2062* (MO); Reserva Biológica Monteverde, Research trail near field station, 10° 18' N, 84° 48' W, 1500 m, *Haber & Zuchowski 9295* (CR); Monte Verde, along Río Guacimal just below Lechería, 10° 17' N, 84° 48' W, 1500 m, *Hammel 13875* (CR,MO); Reserva Biológica Monteverde, Sendero Cascada, 10° 18' N, 84° 47' W, 1550 m, *Ivey 16* (CR); Reserva Biológica Monteverde, Research trail S. of Sendero Nuboso, 10° 18' N, 84° 47' W, 1550 m, *Ivey 21* (CR [2 sheets]); Monteverde, community, trail leading N. from Campbell's Bull Pen, 10° 18' N, 84° 47' W, 1450 m, *Ivey 39* (CR); Reserva Biológica Monteverde, Sendero Chomogo, 10° 18' N, 84° 47' W, 1550 m, *Ivey 46* (CR); Monteverde, Campbell's woods, 1520 m, *Koptur SK-277* (MO); Monteverde Cloud Forest Reserve, off of Nuboso Trail, 10° 06' N, 83° 26' W [sic], 1500 m, *J.F. Smith 530* (CR,F). San José: between Bajo La Hondura and Alto La Palma, 10° 2' N, 83° 59' W, 1400–1500 m, *Barringer et al. 4001A* (CR,F).

Geonoma brenesii comprises solitary, acaulescent, understory palms with spicate inflorescences. The new species closely resembles, and has been invariably confused with, the widespread and variable *Geonoma cuneata* (including *G. gracilis*). It differs from *G. cuneata* in having a comparatively narrow peduncular bract attached high (> 3 cm) above the prophyll and enclosed within it, a densely stellate-pubescent inflorescence rachis (whence the specific epithet), and female flowers with deeply crenately to subdigitately lobed staminodial tubes. In addition, *G. brenesii* is somewhat smaller in stature, with generally smaller leaf-blades, and occurs at higher

elevations than *G. cuneata*, which does not ordinarily surmount ca. 1200 m in Costa Rica. All of the specimens of *G. brenesii* collected to date have exclusively pinnate leaf-blades, never simple and bifid, as is often the case in *G. cuneata*.

The new species perhaps comes closest to *Geonoma paradoxa* Burret, of Pacific Colombia, comprising plants of similar dimensions, spicate inflorescences with the peduncular bract included in the prophyll, and female flowers with the staminodial tube digitately lobed. However, the prophyll and peduncular bract of *G. paradoxa* are attached close together near the base of the peduncle, and the inflorescence rachis lacks the whitish, stellate hairs typical of *G. brenesii*. The recently described *Geonoma hugonis* Grayum & de Nevers, of westernmost Panamá, resembles *G. brenesii* in having spicate inflorescences with the peduncular bract (when present) attached well above the prophyll and female flowers with the staminodial tube digitately lobed. This combination of characters blurs the distinction between *Geonoma* sects. *Geonoma* and *Taenianthera* (Burret) Wess. Boer, as discussed by de Nevers & Grayum (1998). *Geonoma hugonis* differs from *G. brenesii* in its caulescent habit, simple, bifid leaf-blades, obsolete or much reduced peduncular bract attached even higher on the peduncle (usually beyond the orifice of the prophyll), and non-stellate rachis pubescence.

Geonoma brenesii occurs sympatrically with another superficially similar taxon (acaulescent, with spicate inflorescences) that I have identified tentatively as a local variant of *G. hoffmanniana* H. Wendl. ex Spruce [a species that normally has (2-)3-17+ inflorescence rachillae]. This latter taxon, exemplified by *Haber & Bello 7316* (CR), has the peduncular bract attached high above the prophyll, as in *G. brenesii*, but differs in its subglabrous to simply pubescent inflorescence rachis and female flowers with truncate staminodial tubes. Also, the peduncular bract in *G. hoffmanniana* is usually well exserted from the prophyll (indeed, it is often attached beyond its orifice).

The species epithet honors Alberto Manuel Brenes Mora (1870-1948), who made the first collection known to me on 29 September 1925. Brenes, a native and lifelong resident of San Ramón de Alajuela, is one of the most celebrated and prolific collectors of the Costa Rican flora.

GEONOMA TALAMANCANA Grayum, *spec. nov.* TYPE: COSTA RICA.

Limón: Cantón de Limón, Cordillera de Talamanca, N flank of Fila de Matama in headwaters of Río Boyei, 9° 45' N, 83° 19' W, 1200-1300 m, 17 Aug 1995, M. Grayum 11033 (HOLOTYPE: MO-4923462!, MO-4923463!, MO-4923464!; Isotypes: CR!, INB!, K!, NY!).

Species combinatione habitus solitarii acaulescentisque cum inflorescentiae longipedunculatae sine bractea pedunculari a congeneribus diversa.

Stems solitary, obsolete to ca. 1.5 m tall and ca. 1-2 cm diam. Petioles beyond sheath 9.5-30.0(-35.0) cm. Leaf-blades simple and bifid or pinnately compound with rachis 17-43(-58) cm, if simple 44.5-81.0 × 9.0-23.5 cm, oblanceolate, incised distally ca. 2/5-3/5 the total length, with 19-24(-40) primary lateral veins per side, if pinnate with leaflets (1-)2-4(-7) per side, 26-50 cm long (medial ones). Infls. interfoliar, spicate; peduncle 27.5-78.5(-81.5) cm, with no enlarged bracts above

prophyll; rachilla 9–26 \times 0.25–0.50 cm, subglabrous or pubescent with short, appressed, inconspicuous, brownish hairs. Male fls. ca. 3.5–4.0 mm long; stamens 6, the anthers sharply reflexed. Female fls. ca. 3.5–4.0 mm long; staminodial tube subtruncate. Ripe frts. ca. 0.7–0.9 \times 0.6–0.8 cm, obscurely tessellate-striate, broadly ellipsoid to ovoid, black.

Apparently endemic to Costa Rica, Atlantic slope Cordillera de Talamanca, 1200–1600 m; April, August.

ADDITIONAL SPECIMENS EXAMINED. COSTA RICA. Cartago: [Cantón de] Paraisó, Orosi, Muñeco, Finca Kuná, ca. 9° 47' 49" N, 83° 55' 04" W, 1350 m, Blanco *et al.* 456 (USJ). Limón: Cantón de Limón, El Progreso, area de suelos inundados entre 1500 y 1700 m, Fila Matama, 9° 47' 20" N, 83° 07' 30" W, 1600 m, Herrera & Chacón 2785 (CR [2 sheets]).

Geonoma talamancana comprises subcaulescent plants with solitary stems and spicate, interfoliar infls. lacking peduncular bracts. Except for the last-mentioned feature, this species differs only subtly from the widespread and variable *G. cuneata* (including *G. gracilis*), which has a prominent peduncular bract (ca. 11–51 cm long), attached near the prophyll and usually well exerted from it. In the field, *G. talamancana* presents a different aspect by virtue of its comparatively rigid leaf-blades with plicate venation. Furthermore, *G. cuneata* is a lowland species, that rarely if ever surmounts 1200 m elevation, at least in Costa Rica.

Collections of *Geonoma talamancana* have previously been attributed (in herb.) to *Geonoma jussieuana* or its apparent synonym, *G. lehmannii* Dammer *ex* Burret, both based on South American types. Although superficially very similar to the new species, *G. jussieuana* differs consistently (according to descriptions and herbarium material) in having a conspicuous peduncular bract, attached high on the peduncle and well exerted from it. I have examined a wide range of material from Costa Rica (outside the range of *G. talamancana*) and western Panamá determined as *G. jussieuana* or *G. lehmannii*, and have found no other collections definitely corresponding to *G. talamancana*. However, a few specimens with top-snatched inflorescences cannot be identified with certainty.

The absence of peduncular bracts is a highly unusual condition in *Geonoma*, otherwise known only in *G. monospatha* de Nevers (which occurs in Costa Rica) and *G. stricta* (Poit.) Kunth (see de Nevers & Grayum 1998). These species differ substantially from *G. talamancana* in their caulescent, potentially cespitose habit and small inflorescences with short peduncles and rachillae.

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THE ROOT MYCOBIOTA OF WOODY PLANTS

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ABSTRACT

The fungal community of roots can be beneficial, detrimental, or a chance relationship of no significance to fungi and the roots of trees occupying the same soil territory. Interrelationships also are influenced by the physical quality and content of the soil, plant, and animal life present, and other additional members of the microbial population including bacteria, viruses, nematodes, and other micro-organisms. The environment in which the woody plant roots are found is selective due to the physical, chemical, and biological determinants present in the soil. This habitat is also influenced by the weather, the change of seasons, temperatures, light intensity, and diurnal periodicity in the form of rain, snow, fog, and dew, as well as degree, amount, and type of air pollutants that filter into the soil. The environment above the soil line also influences the environment in the soil, and all serve as factors governing the relationships and populations of fungi in association with roots of woody plants.

KEY WORDS: fungal ecology, root mycobiota, forest habitats

The soil - root - woody plant fungal community is a complexity that defies discussion even in a limited evaluation of fungal species present in the environment of the roots. The magnitude of a soil - root study is a topic that does not fit within the scope of a single chapter, therefore discussion is primarily directed to the fungi of roots of woody plants. Interspecific relations of fungi and roots create different degrees of association, residing together in some degree of association. An equilibrium or biotic balance of the fungi and roots could create a steady state of existence in which the root cell area and the fungal mycelium and reproductive cells are held in a fixed ratio of each other. The surrounding environment contains many variables, yet the capacity of fungal density, and root ratio remain somewhat steady, creating a homeostatic state. The relationships of tree roots and soil micro-fungi could range from loose association to close proximity of commensals, organisms that feed

together. One species profits by living together with the other. In commensal relations, one species converts an unavailable substance to an assimilated substance for the other. One species could exude a waste product that the other species associate could utilize or the product could inhibit the growth of potential competitive species. Also, one commensal species could directly provide nutrients, protection, moisture, or shelter for the other. The species could coexist under specific circumstances, both fungus and woody plant could easily, and frequently do, exist separately.

Tree roots and fungi could act as symbionts, each receiving mutually beneficial effects from the other. Both species are helpful to each other and receive an essential part of the microenvironment from the other. These associations could be species specific. A reliance exists, and frequently these associations are limited to individual symbionts which increases the growth rate of both the tree and the fungus. Enhanced metabolic activity of the root and the fungus could result in supplying organic nutrients, generate CO_2 or O_2 , removing O_2 , assimilating N_2 , or providing minute amounts of growth factors. Together the fungus and the tree root could provide physical support, supply inorganic nutrients, utilize metabolic wastes, protect against parasites, and shield against the environment.

Of course the root system of trees and the mycelium of fungi found in the same soil habitat remain in competition for certain nutrients, water, and the space that they occupy together. These organisms remain in rivalry for the same parameters. Parameters contributing to this competition include the rate of growth of both trees and fungi plus the growth of other organisms, both plants and animals inhabiting the soil. Tolerance to abiotic factors present in the same location influences survival and growth. The ability of the woody plants and the companion fungi to multiply, grow, and propagate new roots or hyphae at low concentrations of limiting nutrients influences the living team members. The capability and the efficiency of utilizing limiting nutrients could serve as the chief survival factor of one or both of the organisms present in the shared community. In this common territory, the ability to store and synthesize reserve substances in living cells is also vital to survival for the competing populations. Phosphorus uptake and below ground carbon utilization were measured using ectomycorrhizal *Thelephora terrestris* and non-mycorrhizal *Salix viminalis* L. Phosphorus inflow rates were three times as high for *T. terrestris* root systems as for *Salix* root systems (Jones *et al.* 1991). Nutrient requirements directly affect carbon economics of the woody plants.

At times, a species of a community creates interactions conflicting with other species. One species is suppressed because of toxins produced by the other species. The growth of one species utilizes the nutrients at that location and alters pH of the mutual habitat that interferes or enhances survival of other species present. The production of hydrogen peroxide, ammonia, and nitrite that accumulate during ammonium oxidation, and hydrogen sulfide accumulation occurs due to the presence of living organisms.

Few fungi, considering the total number and diversity of fungal species, function at all times as an obligate pathogen occupying an environment and serving as a disease causing agent on every opportunity for growth. Most fungal species do not cause disease. In a true parasitic association, the host becomes the food source of another organism. When the fungal organism in the soil invades tree root systems, a parasitic relationship becomes established. An opportunity is opened for the fungus existing in

close proximity to roots to establish disease. Frequently, micro-fungi grow in soil on organic matter that comprises the soil particles. Chance contact of the fungus with the root allows the fungal hyphae to associate with living cells of the root. Penetration of cell walls by the hyphae establishes a parasitic relationship, however, only a very limited number of micro-fungi are parasitic and never create an opportunity for living cell invasion.

In deeper layers of soil, fungal activity is generally associated with plant roots. Fungi growing in the vicinity of plant roots are frequently stimulated in growth compared to fungal species in soil away from the influence of roots (Barton 1957). The rhizosphere effect of roots of higher plants was discovered by Hiltner (1904). The rhizosphere root soil complex contains organic substances released from roots that stimulate micro-fungi spore germination as well as hyphal growth (Jackson 1957). Sterile mycelial forms are commonly found associated with roots of woody plants, presenting no obvious beneficial or detrimental association with the plants (Harley *et al.* 1955). Organic matter which accumulates in soil from roots is composed of insoluble cell wall debris, polysaccharide mucilages secreted by root cells, mucilages formed from polysaccharide hydrolysates of cell walls, and water soluble exudates given off by root tissue (Foster & Rovira 1973). Vitamins, enzymes, growth hormones, and other organic substances are found in plant exudates. Volatile organic acids, aldehydes, and unsaturated fatty acids are also produced by roots that inhibit and at times stimulate fungal growth (Fries 1973). Ethylene can be produced by roots which also regulates growth of micro-fungi (Burg 1962). Mucigel polysaccharides found on root caps are a rich source of substrates for micro-fungal as well as bacterial growth (Greaves & Darbyshire 1972).

Fungistatic properties of soil keep most fungal propagules under control through microbial competition and soil nutritional limiting factors retarding the growth of the organism. The stimulation of micro-organisms in the rhizosphere is caused by the presence of an increased supply of nutrients in the form of soluble inorganic and organic root excretions (Jackson 1960). The breakdown products of sloughed-off dead root cells, lowering of the concentration of certain mineral elements in the soil due to their absorption, soil desiccation from water absorption, and increase in soil carbonates following carbon dioxide production by the roots all directly relates to the rhizosphere community (Starkey 1929). However, a very high percentage of fungi in soils are present as inactive propagules (Warcup 1955). Sugars induce the germination of inhibited fungal spores, and these carbon sources are produced by root excretions by seedlings in quantities sufficient to have stimulating effects on the soil populations of fungi. Excretion of sugars occurs primarily in the young meristematic regions of roots (Jackson 1960). The rhizosphere effect itself may be studied along two broad lines, one concerning the plant influence on soil micropopulations, the other dealing with the influence of the rhizosphere microflora on the plant (Katznelson 1960).

Microflora populations in the rhizosphere increase as plants age. Greater quantities of organic matter become available through aging and death of plant roots for the growth of micro-fungi in the soil (Peterson 1958). Older roots are more vulnerable to damage by soil particles and invasion by micro-fungi into epidermal and cortical cells adjacent to the mucigel sheath (Old & Nicholson 1975). In woody plant roots, primary cortex is sloughed off during secondary growth which adds to the organic concentration in the rhizosphere of older trees. It was concluded that half of the root

system of apple trees (*Malus* spp.) is lost as cortical tissue each year (Rogers 1968). Also, the natural death of young root system of mature plants and of major branch roots also adds to the carbon, nitrogen, and mineral content of the rhizosphere, enhancing the growth of micro-fungi. Several hundred kilograms of biomass per hectare of soil accumulates from decomposing root systems (Head 1973).

Changes in tree physiology induced by environmental changes is also influential on rhizosphere micro-fungi populations. Beach (*Fagus sylvatica* L.) root surface fungi undergo significant changes (Harley & Waid 1955b). Low light intensities increase root colonization of *Cylindrocarpon* and *Rhizoctonia* species, while high light intensities increase populations of *Trichoderma* and *Gliomastix* species. Light intensity and temperature also influence the amount and availability of amino acid and organic acid content of exudate production (Rovira 1959; Smith 1972). Desiccation increases amino acid exudate release through roots to the soil adding to nutrients available for soil micro-fungi. Phosphorus (Katznelson *et al.* 1954), potassium (Rovira & Ridge 1973), and nitrogen (Bowen 1969) added to the soil as fertilizer also change exudate production in the root system and the amount of nutrients for the growth of fungi, depending on plant species, plant age, and various soil qualities. Soil micro-fungi interactions and associations with other micro-organisms in the rhizosphere are discussed in detail by Brown (1975), Curl & Truelove (1986), Mosse (1975), and Hale *et al.* (1978).

Root infection by fungi consists of an infinite series of gradations between primitive facultative parasite and obligate parasite associations (Garrett 1960). Most root associations by fungi are saprophytic, with few species causing disease in woody plants. The classic example of tree root disease in forest trees is *Armillaria mellea* root rot, first described in 1873 (Hartig 1873). Another classic parasite is gummosis disease of citrus, caused by *Phytophthora citrophthora*, first investigated in 1878 and continued through 1949 (Fraser 1949). The fungal attack is gradual and starts in young rootlets, slowly migrating upwards, finally exhausting the tree. The persistent *Armillaria* can remain six years or more in infected citrus roots of less than 30 mm in diameter (Bliss 1951). Carbon disulphide soil fumigation was first used to control *A. mellea* in infected roots, a method used for over 40 years. However, as *A. mellea* decreased in dominance, *Trichoderma viride* gradually increased to become the dominant soil borne fungus (Warcup 1952). Formalin treatment of soil also promoted dominance of *T. viride* which proved to be a much more tolerant fungal species with tree root association. When *Fomes lignosus*, *F. noxius*, and *Ganoderma pseudoferreum* infecting roots of rubber trees were controlled by dichloropropano-dichloropropylene treatment, this action also brought a similar dominance of *T. viride* in the soil (Altson 1950). Further study indicated chemical control of the fungal pathogens was less significant, but the antibiotic activity of *T. viride* was more effective in the soil habitat (Weindling 1941; Weindling 1934; Weindling 1932).

A succession of fungi is noted in soil substrates (Garrett 1960). Substrates in all habitats, including soil, are in constant change, replacement, and depletion. Root surface micro-fungi exist topically and survive as epiphytes (Hiltner 1904). Initial invasion of the root surface is made by a sequence of saprophytic sugar fungi. Next in sequence are the cellulose decomposers, and finally the lignin-decomposing fungi invade root tissue. An ordered succession under continual change occurs. Maximum destruction of host tissue occurs when fungal parasites overwhelm the resistance of mature host plant roots in full growth vigor. The most vigorously growing trees

quickly succumb to fungal attack at the soil level by these destructive parasites (Waterston 1941). Species of *Rosellinia* found in the tropics as a saprophyte in surface litter under heavy shade can easily revert to becoming a destructive tree root invasive parasite.

Many of the tree root-inhabiting fungi exhibit an ectotrophic growth habit in that the invasion is continuous and indefinite over the host root system (Garrett 1960). *Fomes lignosus* and *Poria hypolateritia* behave in this way also (Petch 1928). In rubber plantations of Malaysia, *F. lignosus* was found to grow through the soil on continuous surfaces such as boulders and dead roots, however, nourishment was through infecting living roots (Napper 1932). It was also observed that sporophores of *F. annosus* may be attached to rootlets so fine that the attachment escapes notice, giving rise to misconceptions that *F. annosus* could live as a saprophyte on forest litter (Risbeth 1951). In reality it is a specialized root-inhabiting parasite of conifers and other trees.

The efficiency of rhizomorphs of *Armillaria mellea* from wood origins is quite remarkable. The strands can grow freely through the soil, extending 22 yards from an infected pit-prop in a mine-working (Ellis 1929), and 30 feet in a water tunnel leading out of a reservoir, in hard rock 200 feet below ground level (Findlay 1951). Rhizomorphs extend in all directions through the soil from a food base of infected wood. Nutrients are supplied by the wood but the soil gives support and possible water and mineral uptake as well. It was learned that ethanol and other short chain alcohols stimulate rhizomorph production (Weinhold 1963). The bulk of *A. mellea* rhizomorph growth requirements are obtained from root tissues, the quality of which may greatly influence rhizomorph production (Redfern 1970). When conifers are wounded or infected, the neighboring tissue frequently becomes impregnated with resin. Artificial infection of two blue-stain fungi (*Ceratocystis ips* and *C. minor*) was successful in pine trees with low resin exudation pressure but not in those with medium or high pressure (Mathre 1964). Volatile components of *Pinus ponderosa* Douglas ex Lawson & C. Lawson resin are toxic to *Fomes annosus* (Cobb et al. 1968). Also, the pinosylvin in infected sapwood of pine have mild fungitoxic properties to *F. annosus* infection (Shain 1967).

Fungi of soil and rhizosphere habitats, fungal distribution in soil, fungal activity in soil, root colonization and root diseases are topics of increased attention in later years. The volume of literature is astronomical (Dix & Webster 1995). Likewise, mycorrhizae are receiving increased attention in soil structure and biogeochemistry, soil reclamation, and biocontrol measures (Pfleger & Linderman 1994). More attention is also directed to the tropical forests of the earth as they relate to the whole earth ecology. Mature tropical forests of rubber [*Hevea brasiliensis* (Willd.) ex A. Juss.] Müll. Arg.], teak (*Tectona grandis* L.f.), and palms (*Elaeis guineensis* Jacq., *Cocos nucifera* L.) have a few pathogenic root lignicolous fungi such as *Rigidoporus lignosus*, *Ganoderma* spp., *Armillaria* sp., *Phellinus noxius*, *Sphaerostilbe repens*, and *Ustulina deusta*. Many other fungi are saprophytic or weak parasites such as *Favolaschia thwaitesii*, *Pycnoporus sanguineus*, *Hexagona apiaria*, *Dacryopinax spathularia*, *Auricularia polytricha*, *Cookeina sulcipes*, and *Phellinus gilvus* (Intini 1991).

It has been recently shown that ectomycorrhizal fungi of tree roots and shoot biotrophs are more host specific than root necrotrophs. Woody hosts are associated

with a greater number of mutualistic fungi than antagonistic fungi. Some hosts are resistant to fungal invasion and others are quite susceptible (Borowicz & Juliano 1991). Ectomycorrhizal fungi colonize roots and are not affected by the presence of saprophytic fungi. The ectomycorrhizal species tend to be more dominant than the saprobes (Shaw *et al.* 1995). Soil borne mycorrhizae fungi also are associated with and closely monitored for the crop production of Chile's citrus industry (Jiménez & Gallo 1993).

Ectotrophic growth patterns of the fungi in roots evolved into mycelial sheets or strands, or into rhizomorphs, or into individual hyphal threads. The growth variations are in response to overcome host resistance to infection by the tree roots (Garrett 1970). Rhizomorphs of *Armellaria mellea* grow from an apical meristem (Motta 1967). Density of the branching increases with the increase in nutrients to an optimum value, forming a fibrous growth pattern. Growth rate of rhizomorphs is much greater than unorganized individual hyphae of the same species. Mycorrhizae are widely distributed among the phanerogams. Only about 3% of phanerogams exhibit ectomycorrhizae, most belong to the endomycorrhizae (Meyer 1973). Various chemical compounds are involved in the formation of mycorrhizae such as orchinol (Gaumann *et al.* 1960).

Many trees would not be capable of developing massive sizes without the symbiotic relationship of the root-inhabiting fungi. Without mycorrhizae, pine trees would be more aptly considered pine bushes. Obligate ectomycorrhizal trees include the genera *Abies*, *Larix*, *Picea*, *Pinus*, *Carpinus*, *Fagus*, and *Quercus* (Meyer 1968). More typical facultative ectomycorrhizal genera are *Cupressus*, *Juniperus*, *Salix*, *Betula*, *Corylus*, *Alnus*, *Ulmus*, *Pyrus*, *Acer*, and *Eucalyptus* (Meyer 1973). These trees survive well in the absence of ectomycorrhizal fungi. Endomycorrhizal trees are abundant in tropical forests of the lowlands, ectomycorrhizal trees are frequently pioneers on wastelands. Endophytic infection development by *Glomus* in sugar maple roots revealed changes in cortical cells similar to other woody plant hosts. Large intracellular hyphae enter the cortical tissue while arbuscules formed from initiation points at various places on the intracellular hyphae (Yawney & Schultz 1990). The arbuscules in the roots are the sites of transfer between the host and endophyte.

Mycorrhizal root association by fungi was first observed by Frank (1885). The benefits of this symbiotic association are numerous and the extent of these associations in the literature of early investigators is well reviewed by Rayner (1927) and Kelley (1950). Mycorrhiza are classified into two groups. Ectomycorrhiza fungi form a mantle around roots and intercellular hyphae grow within the root cortex. Forest tree associations are ectotrophic and most of the fungi are Basidiomycetes. Endotrophic mycorrhizae are inter- and intra-cellular in the host cortical cells.

Due to the growth patterns, ectotrophic mycorrhizal fungi are considered to have evolved from specialized root pathogens (Garrett 1970). Of equal possibility, these specialized symbionts may have evolved from saprophytic root surface fungi (Harley 1948). The growth relations of these fungi have developed an efficient mechanism in quite a delicate balance of host-parasite association and host-resistance tolerance. Further characterizing this fungal growth, infection of short roots is truly ectotrophic with a fungal mycelial sheath covering the root surface. Long roots are penetrated internally as an extension of the Hartig net of fungal tissue internally in the host root cortex (Robertson 1954). Two modes of ectotrophic infection of *Fomes annosus* on

Pinus sylvestris L. (Scots pine) are possible (Risbeth 1951). In alkaline soils, the fungus grows freely on the root surface, forming pronounced sheet-like mycelial aggregates. Acid soils delay or totally suppress epiphytic mycelium, and slows infection with the root cylinder infections at times ahead of the epiphytic growth. Ectotrophic advance on the outside of roots in alkaline soils is much ahead of the fungal growth in acid soils (Wallis 1961).

Douglas fir [*Pseudotsuga taxifolia* (Lamb.) Britton], larch (*Larix decidua* Mill.), and spruce [*Picea abies* (L.) H. Karst] resistance to inner wood tissue infection is lower than that in species of pine, so infection is more severe (Risbeth 1951). Fungal growth from saprophyte to parasite is definite per tree genus, following defined patterns from initial infection to advanced tree disease. The degree of resistance to infection from *Fomes annosus* in pines is correlated with the complexity and activity of resin canal systems (Gibbs 1968; Gibbs 1967). The toxicity factor of resin to *F. annosus* and four timber bluestain fungi was studied (Cobb *et al.* 1968). Crude oleorecin and components of the volatile turpentine fraction, purified by fractional distillation reduced hyphal growth of *F. annosus* and the bluestain fungi by various degrees when the fungi were exposed to a vapor saturated atmosphere. The nine terpentine components were identified as two monocyclic, four bicyclic, and one open-chain terpene, and two alkanes. The alkane n-heptane was the most fungistatic, completely inhibiting hyphal growth of *F. annosus* and the wood bluestain fungus *Ceratosystis pilulifera*.

Tree mycorrhizal formation and structure is directly associated with many factors affecting root development (Marks & Foster 1973). These factors include fertilizers (Zottl 1964), light (Kinugawa 1965), girdling, decapitation, and defoliation of shoots (Richardson 1953), temperature (Barney 1951), soil moisture and aeration (Mikola 1967), auxins (Slankis 1958), minerals (Davis 1949), bacterial physiology (Wichner & Libbert 1968), root disease (Zak 1964), and carbon, vitamin, and nitrogen source (Gibson 1961). An ecto- endomycorrhizal condition is common in aging mycorrhizae with the intracellular penetration of cortical cells (Marks & Foster 1967). One mycorrhizal type can be replaced by another when root growth resumes after a dormant period.

Mycorrhizal partnership can form between a single tree species and a number of different fungi (Zak & Marx 1964). Like roots, shoots, and individual hyphae, rhizomorphs grow from the apex of the structure, as long as minerals are present, provided by the host root and the soil through which it is passing. Rhizomorphs will continue to grow only for as long as the apices are covered by an unbroken film of water (Griffin 1969). The presence and importance of mycorrhizae in forest soils is the mutual support the trees and fungi have for each other, the subject of symbiosis between autotroph and heterotroph (Harley 1975).

Alkaline soils as compared with acid soils allowed for more rapid growth of *Fomes annosus* (Risbeth 1950), and moisture stress increased susceptibility of *Pinus taeda* L. (loblolly pine) to infection (Towers & Stambaugh 1968). Growth inhibition and antagonism caused by bacteria and other fungi against another fungus takes place in the root zone. The degree of *Trichoderma viride* antagonistic effects against *F. annosus* is related to particular strain isolates (Mughogho 1968). Forest root exudates contain a combination of amino acids, carbohydrates, and organic acids according to species and soil type (Smith 1969). The concentration of exudate in the rhizosphere

depends on rate of movement in soil and uptake by micro-fungi. The rhizosphere of young fir seedlings contains 0.3 (in millions) total number of fungi in 1 g soil, overcrowded prime firs contain 0.02, old firs (*Abies alba* Mill.) 0.08, and in the soil of a fir plantation 0.065 (Maliszewska & Moreau 1960). There is a more varied flora in the soil and rhizosphere of young firs. *Trichoderma viride* is present in soil around roots of young firs, also in soils carrying a good regeneration. This species is absent in soils offering a poor regeneration of fir seedlings, and in the rhizospheres of old trees. The presence, and often abundance of *T. viride* can serve as the index of soil fertility for a wide variety of plant species.

Tree seedling fungal studies have been contained in controlled environments in the laboratory and controlled plots in nature for a better understanding of study parameters. Seedlings of live oak (*Quercus virginiana* Mill.), Chinese tallow tree [*Sapium sebiferum* (L.) Roxb.], and Texas mountain laurel [*Sophora secundiflora* (Gomez-Ortega) Lagerh. ex DC.] were inoculated with either ectomycorrhizal fungi (*Pisolithus tinctorius*) or vesicular-arbuscular mycorrhizal (VAM) endomycorrhizal fungi (*Glomus fasciculatum*, *Gigaspora margarita*, and *Glomus mosseae*) and transplanted into nature (Davis & Call 1990). The inoculated trees showed greater growth and survival than non-inoculated controls. Under controlled conditions, in roots of lodgepole pine seedlings, some competition in root association is noted by ectomycorrhizal and saprotrophic fungi (Shaw *et al.* 1995). The saprotroph *Collybia maculata* significantly retarded rate of colonization of lodgepole pine seedling roots by *P. involutus*.

Hundreds if not thousands of species of both macro- and micro-fungi reside in soil habitats making part if not all their life cycles in the soil environment. Roots of woody plants, as well as grasses and herbaceous species, create microenvironments for the establishment and growth of fungal hyphae and spore structures depending on the family and order to which they belong. The root cap is a protective region of the meristematic end of the root which per surface volume sloughs off the greatest quantity of cells into the sod as the root extends farther from the tree trunk and deeper into the soil. These sloughed off cap cells provide a rich carbon and nitrogen source of nutrients immediately around the root tip for the establishment of fungal growth. One saprophytic species by chance in the vicinity of the root begins growth in the enriched soil. Spores or other fungal elements of other species of micro-fungi soon establish themselves in close proximity to the growing roots. One or more species becomes dominant in the root environment according to the quantity and quality of nutrients accumulated as waste material from the woody and herbaceous plants. Established micro-fungal species present also add to the soil nutrients as waste products are produced and dead fungal cells accumulate in the root environment. A distinct micro-environment begins to evolve around the roots which supports the growth of other fungi and other microbes as they become established in the community.

Epidermal cells and cortical cells, resins, suberins, high molecular weight carbon compounds, nitrogen, and vitamins become available to the root environment as the fungal populations evolve, as new species become dominant and established species fade away. This material from the trees is deposited in the soil immediately adjacent to the root surface and remains in high concentrations around the expanding root as growth in circumference continues during each growing season of the tree. Deuteromycetes remain the dominant species of the saprophytic community but some specialized Basidiomycetes, Ascomycetes, and Phycmycetes are found in a root

bound community of micro-organisms according to other physical factors in the soil such as moisture content, aeration, available minerals, and varying relationships of the fungal species with the tree roots. Needle leaf tree species generally are devoid of root hairs and fungal hyphae form a symbiotic attachment with the tree roots. The fungus benefits from the relationship by obtaining glucose and other carbon sources from the tree supplied by photosynthesis. The tree benefits from the presence of the fungal hyphae by greatly increasing the surface to volume ratio capacity of the roots for the absorption of water and minerals into the host plant.

Host specific fungi are brought into the soil micro-environment with the establishment of various trees. The more broad spectrum saprophytes that grow equally well on many carbon and nitrogen sources establish their growth without the presence of host trees (Volz *et al.* 1992). Some of these fungi readily grow on organic material originating from human or animal sources, yet pathogenicity is not established unless the fungus is introduced into a potential host (Volz *et al.* 1993). Mycorrhizal fungi are mostly symbiotic, benefitting both themselves and their hosts as they grow together. If a fungal species penetrates the host root cortical or vascular system, a pathogenic relationship is established that could extend through the roots into the above ground portion of the tree such as the wood rot fungi to ultimately cause death to the tree or part of the tree. The tree species may have the capacity to outgrow its invader for a period of time, but survival is made more difficult under harsh environmental and seasonal changes experienced by the host tree. Eventually over a period of years, the tree will lose the battle to survive growth of the invading fungus pathogen, and death to the tree will occur. However, most fungal species found in the soil are micro-fungi that utilize organic matter and cause no harm to the tree species or other plants and animals of the forest (Volz *et al.* 1994).

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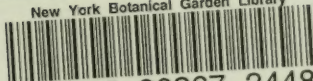
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NEW NAMES IN THIS ISSUE OF PHYTOLOGIA

As a result of the International Botanical Congress in Tokyo in 1993, the International Association of Plant Taxonomy has been tasked with exploring the feasibility of registration of plant and fungi names. In accordance with terms of the pilot implementation of the registration concept, new names and combinations produced in this issue of PHYTOLOGIA are listed below.

| New name or combination | Page Number |
|--|-------------|
| <i>Mandevilla rugellosa</i> (Rich.) L. Allorge, <i>comb. nov.</i> | 305 |
| <i>Bactris polystachya</i> H. Wendl. <i>ex</i> Grayum, <i>spec. nov.</i> | 308 |
| <i>Calyptrogyne herrerae</i> Grayum, <i>spec. nov.</i> | 309 |
| <i>Chamaedorea hodelii</i> Grayum, <i>spec. nov.</i> | 312 |
| <i>Geonoma brenesii</i> Grayum, <i>spec. nov.</i> | 322 |
| <i>Geonoma talamancana</i> Grayum, <i>spec. nov.</i> | 324 |

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Information for Authors

Articles from botanical systematics and ecology, including biographical sketches, critical reviews, and summaries of literature will be considered for publication in PHYTOLOGIA. Manuscripts may be submitted either on computer diskette, or as clean typescript. Diskettes will be returned to authors after action has been taken on the manuscript. Diskettes may be 5.25" or 3.5" and may be written in any IBM or Macintosh compatible format. Typescript manuscripts should be single spaced and will be read into the computer using a scanner. The scanner will read standard type fonts but will not read dot matrix print. Manuscripts submitted in dot matrix print cannot be accepted. Use underscore (not italics) for scientific names. Language of manuscripts may be either English or Spanish. Figures will be reduced to fit within limits of text pages. Therefore, figures should be submitted with internal scales. Legends for figures should be included in figures whenever possible. Each manuscript should have an abstract and key word list. Specimen citations should be consistent throughout the manuscript. Serial titles should be cited with standard abbreviations. References cited only as part of nomenclatural summaries should not appear in Literature Cited. Nomenclatural work should include one paragraph per basionym and must provide proper (as defined by the current *International Code of Botanical Nomenclature*) citation of sources of epithets and combinations.

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